Beef Cattle Breeding

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PREFACE

This publication was prepared to acquaint beef cattle breeders and students of the beef cattle industry with genetic principles and procedures for making genetic improvement. Genetic improvement can be maximized by combining selection from purebred herds that provide seedstock to commercial breeders who practice systematic crossbreeding.

For within breed or seedstock improvement, a systematic record of performance program is fundamental to genetic improvement in beef cattle. A clear understanding of genetic principles is essential for developing the most effective selection programs using such records. The commercial beef producer has the opportunity to further improve efficiency of production and desirability of product through systematic crossbreeding. Crossbreeding can be used to take advantage of substantial benefits of heterosis or hybrid vigor and to combine and match desired characteristics of breeds with market requirements and with feed and other resources available in different herds or production situations. A working knowledge of the genetic basis for the benefits of heterosis and the differences between breeds and various systems of crossbreeding that can be used to increase efficiency of commercial beef production are discussed in this publication.

The principles of genetic improvement through selection based on performance records, as well as systematic crossbreeding discussed in this publication, are based on results of research with beef cattle and other species. Much of the material that pertains specifically to beef cattle has evolved from the three regional research projects on beef cattle breeding. These three regional research projects are cooperative between State agricultural experiment stations and the Agricultural Research Service, U.S. Department of Agriculture, in the North Central, Western, and Southern regions.

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BEEF CATTLE BREEDING

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The major objective of agriculture is the effective use of land. More than half of the land area in the United States is in grass. Beef cattle convert a large part of the production of this enormous land area into a palatable and nutritious product. More specifically, they convert the feeds produced on individual farms and ranches into a product in demand by consumers.

The major ways of improving productive efficiency and carcass desirability of beef cattle are through a knowledge of breeding, feeding, disease control, marketing, and management. This publication is concerned only with breeding, but a knowledge of all these areas is fundamental to the economical production of highly desirable beef. These

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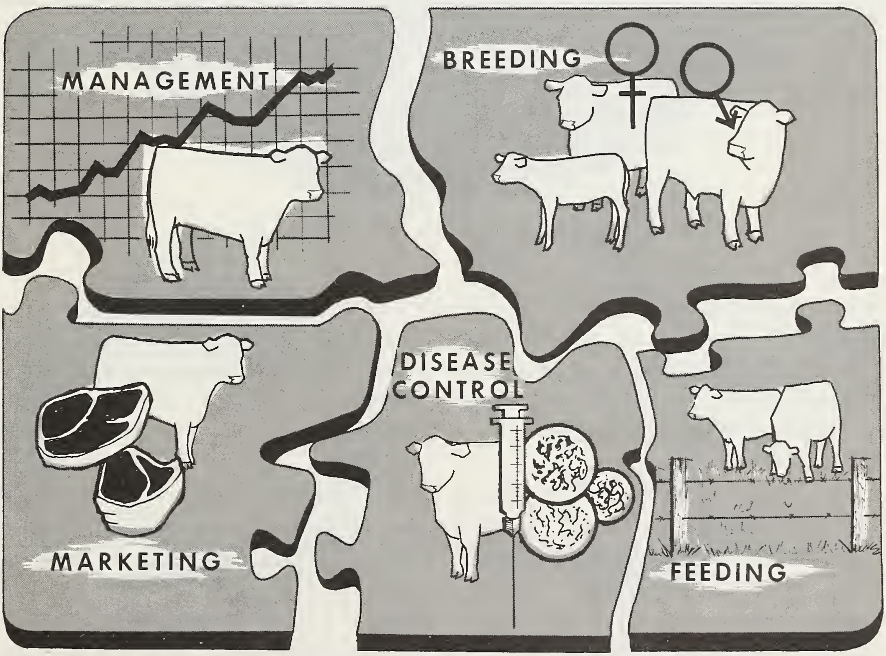
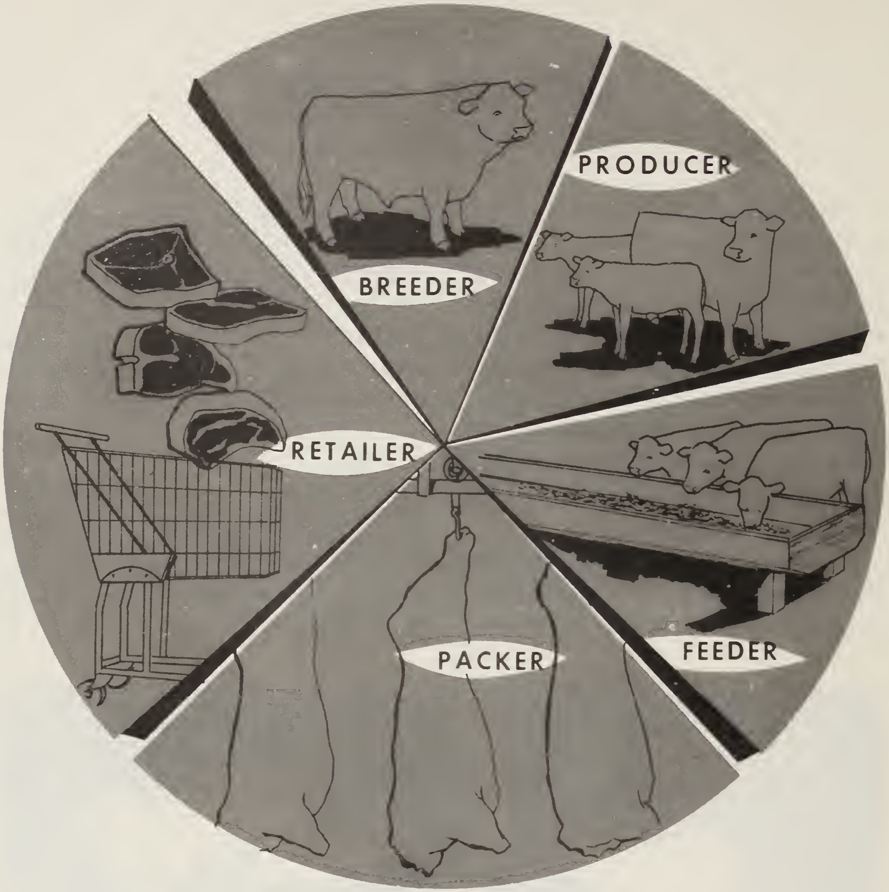


Major factors that contribute to efficient production and carcass desirability in beef cattle.



All segments of the beef cattle industry are interdependent.

areas may be viewed as a jigsaw puzzle, each part of which contributes to completion of the picture of more beef production with greater consumer desirability.

The beef cattle industry in the United States is composed of these segments: (1) the purebred breeder or seedstock producer, (2) the commercial producer, (3) the feeder, (4) the packer, and (5) the retailer.

The purebred breeder of beef cattle maintains seedstock herds to provide bulls for the commercial producer. The commercial producer provides feeder stock to the feeder who, in turn, provides the packer with finished beef cattle ready for slaughter. The packer slaughters the cattle and provides the retailer with either dressed carcasses or wholesale cuts from these carcasses. The retailer breaks down the dressed carcasses, or wholesale cuts, into retail cuts, which are trimmed and packaged

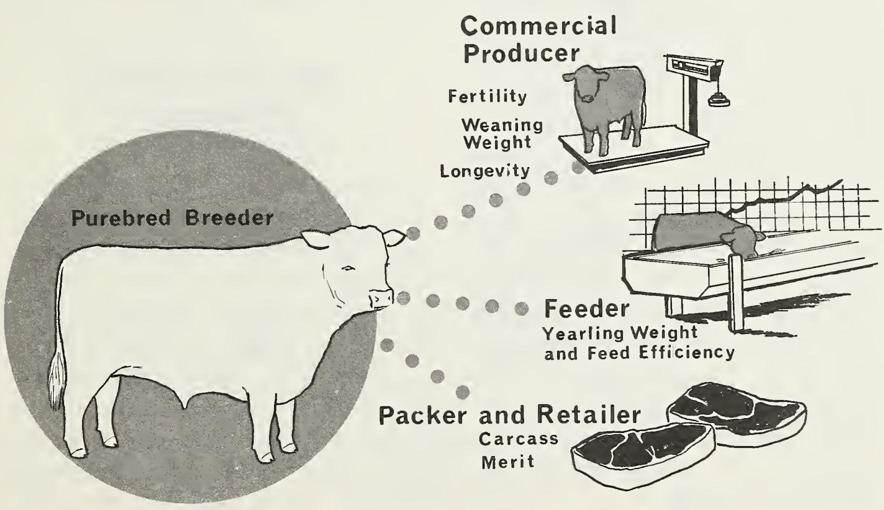
suitably for his customers, the consumers.

An interdependence exists among these segments because each affects cost of production or desirability of product, or both. Both desirability and price of product are reflected in changes in consumption. In fact, level of consumption is important to all segments. Once a product is established, beef consumption depends primarily on how much it costs consumers relative to other food items and how well they like it. Therefore, the profits that accrue to all segments of the beef cattle industry depend on continued improvement in productive efficiency and carcass desirability.

Only traits that contribute to productive efficiency and carcass desirability are of major economic importance to the beef cattle industry. These economically important traits, frequently referred to as performance traits, are: (1) fertility, (2) calving difficulty, (3) mothering or nursing ability, (4) rate of gain, (5) efficiency of gain, (6) longevity, and (7) carcass merit.

RESPONSIBILITY OF THE PUREBRED BREEDER AND THE COMMERCIAL PRODUCER

Expanding human populations will result in an increased demand for beef if present levels of consumption are maintained or expanded. The increase in population and the decrease in land available for beef production give impetus to increased productive efficiency. Further reductions in production costs relative to other foods are necessary if beef is to maintain and improve its position among other high-quality protein foods. Additional improvement in product desirability will aid greatly



The purebred breeder is concerned with making genetic improvement in all traits of economic value in beef cattle.

in maintaining and improving the current acceptance of beef.

The opportunity for genetically improving production efficiency and product desirability rests in the hands of purebred breeders and commercial producers. They determine the matings that produce beef and replenish breeding stock. Improved breeding practices based on selection in purebred herds that provide seedstock to commercial producers who practice systematic crossbreeding will contribute substantially to increased productive efficiency and desirability of product.

Selection is the primary tool available to purebred breeders or seedstock producers for making genetic improvement. Most of the opportunity for selection in beef cattle is among bulls. In addition to benefits from systematic crossbreeding, level of performance and rate of improvement in commercial beef cattle populations is determined primarily by the bulls available to commercial herds from the purebred segment of the industry. To fulfill his responsibility to the other segments of the beef cattle industry, the purebred breeder or seedstock producer should have a working knowledge of genetics, or the science of heredity, along with an appreciation of all traits of economic importance to the industry. In addition, he should understand the procedures for measuring or evaluating differences in these traits and be able to develop effective breeding practices for making genetic improvement in them.

The commercial producer has the opportunity to improve efficiency of production and desirability of product further through systematic crossbreeding. Crossbreeding provides for hybrid vigor or heterosis to increase survival, reproductive performance, mothering ability, growth rate, and longevity. Crossbreeding can also be used to combine and synchronize desired characteristics of breeds with market requirements, feed, and other resources available in different herds or production situations. A working knowledge of the benefits and genetic basis of heterosis, differences between breeds, and systems of mating are needed by commercial producers to develop more effective breeding programs.

This publication outlines some of the basic principles of genetics to improve beef cattle. First, those relating to within-breed improvement based on selection will be reviewed; then, principles relating to crossbreeding by commercial producers will be discussed.

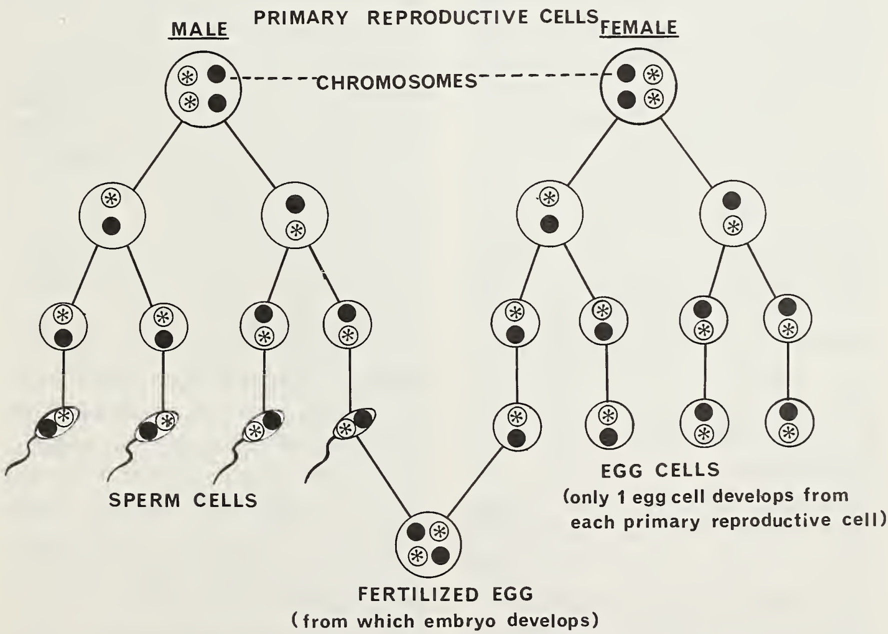
BASIS FOR GENETIC IMPROVEMENT

Differences among animals result from the hereditary (genetic) differences transmitted by their parents and the environmental differences in which they are developed. With minor exceptions, each animal receives half its inheritance from its sire and half from its dam. Inheritance units are known as genes and are carried on threadlike material, present in all cells of the body, called chromosomes. Cattle have 30 pairs of chromosomes. The chromo-

somes and genes are paired, each gene being at a particular place on a specific chromosome pair. Thousands of pairs of genes exist in each animal, and one member of each pair comes from each parent. All cells in an animal's body have essentially the same makeup of chromosomes and genes.

Special kinds of tissue in the ovaries and the testicles produce the reproductive cells, which contain only one member of each chromosome pair. Which gene from each pair goes to each reproductive cell is purely a matter of chance. In this halving process, a sample half of each parent's inheritance goes to each reproductive cell. The genetic potentialities of an individual are determined at fertilization. Pairing of chromosomes restores the full complement when a reproductive cell from the male fertilizes a reproductive cell from the female. This restoration keeps the number of chromosomes constant over countless generations. Because the half of each of its parents' inheritance that each reproductive cell receives is strictly a matter of chance, some reproductive cells will contain more desirable genes for economically important traits than will others.

The union of reproductive cells that contain a high proportion of desirable genes for economically important traits results in a superior individual and offers the opportunity for selection. Chance segregation in the production of reproductive cells and recombination upon fertilization



Production of reproductive cells and fertilization (only two pairs are shown).

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are the cause of genetic differences among offspring of the same parents.

The genetic merit of a large number of offspring will average that of their parents. However, some individuals will be genetically superior to the average of their parents; an approximately equal number will be inferior. Those that are superior provide the opportunity for selection and genetic improvement. The basis for genetic improvement is differential reproduction, which is accomplished by permitting some animals to leave a greater number of offspring than others or by permitting some to leave offspring while others do not. This is what happens when selection is practiced.

Genes vary greatly in their effects. Some traits are controlled primarily by a single pair of genes, whereas, other traits are affected by many genes. Dwarfism and color are examples of traits controlled primarily by a single pair of genes. Most of the economically important traits—carcass characteristics, growth rate, feed efficiency, and mothering ability—are affected by many genes. The thousands of genes present make countless combinations possible in any animal. Because genes are too small to identify individually, they manifest their presence by such outward effects as differences in growth rate, feed efficiency, and conformation.

In traits controlled by a single pair of genes, one member of the pair may be dominant. The dominant gene has the capacity for covering up, or masking, the effect of the other member of the pair. The gene masked is referred to as recessive. For example, the gene for polled masks the gene for horns when both are present. Polled is dominant; horned is recessive. Also, the gene for dwarfism is recessive to the gene for normal appearance. For example, if N represents the gene for normal appearance and n represents the gene for dwarfism, individuals with the genetic makeup of NN and Nn are normal in appearance, but Nn individuals carry the gene for dwarfism and transmit this gene to approximately half their offspring. Dwarfs (nn individuals) can result from mating normal-appearing parents if each carries the gene for dwarfism (Nn $\times$ Nn). Mating normal-appearing individuals that carry the dwarf gene (Nn $\times$ Nn) results in noncarriers (NN), carriers (Nn), and dwarfs (nn) in a 1:2:1 ratio.

Among animals, all differences that are not genetic are classified as environmental. Even though every attempt is made to provide a uniform environment, random environmental differences still exist among animals. For example, identical twins are exactly alike in their genetic makeup but differ in their performance because of random or chance environmental differences. All animals are not at exactly the same place at the same time, grazing the same area, or exposed to the same environmental elements. Some members of a group may contact infectious organisms while others do not. Another example might be injury to the udder of a cow, which would reduce her milk production

and result in decreased weaning weight of her calf. Many random environmental factors may affect some members of a group and not others, thus affecting the expression of differences in economically important traits.

GENE FREQUENCY

The objective of selection for any performance trait is to increase within the herd the number or frequency of desirable genes affecting that trait. This is accomplished by selecting animals that are above herd average in genetic merit.

Differential reproduction is the basis for change in gene frequency and genetic improvement. Culling animals that are poor in economically important traits reduces the frequency of undesirable genes in a herd when the culled animals are replaced by animals that are superior in those traits and thus have a higher percentage of desirable genes. Differential reproduction is the basis for continuous livestock improvement. The increase of desirable genes in one generation is added to those of the previous generation. For this reason, genetic improvement tends to be permanent.

Gene frequency refers to the percentage of the available locations that a particular gene occupies in a herd or population. Because genes are paired in each animal, gene frequency includes both members of each pair and ranges from 0.00 to 1.00. For example, when a herd is free of dwarfism (NN), frequency of the dwarf gene in the herd is 0.00, and frequency of the gene for normal condition is 1.00; it occupies every potential location. Conversely, in a herd of dwarfs (nn), frequency of the dwarf gene is 1.00 and frequency of the gene for normal condition is 0.00. In a herd where all the animals are carriers of the dwarf gene (Nn), the frequency is 0.5 for both genes. Thus, the combined frequencies of both members of a gene pair are 1.00.

GENETIC VARIATION

Genetic variation is caused by either additive or nonadditive effects of genes. When genes produce their effects in a manner comparable to adding block upon block, as in construction of a building, their effects are referred to as additive gene effects. The additive effects of genes affecting a trait combine to determine an animal's *breeding value* for a specific trait. Parents transmit a sample of one-half of their genes to their offspring; therefore, the average performance of an animal's progeny measures half of his breeding value relative to other progeny groups in a contemporary environment. The result of selection is to increase the frequency of desirable genes that produce additive effects. The proportion of total variation (genetic and environmental) caused by additive gene effects is called heritability.

Nonadditive gene effects are caused by interaction of genes. These occur when specific pairs or combi-

nations of genes produce favorable effects as a result of being present together in the individual. When specific pairs of genes produce a favorable effect, the result is referred to as heterosis or hybrid vigor. Within a breed, parents cannot consistently transmit these effects to their offspring because only half of their genes, one of each pair, is passed on to the next generation. However, systematic mating procedures involving different breeds can be used to restore favorable nonadditive genetic effects from one generation to another.

Traits vary in the degree to which they are controlled by these two kinds of genetic variation. For traits where most of the genetic variation is additive because of differences in breeding value and where environmental variation is relatively low, selection between and within breeds will be effective. For traits where most of the genetic variation is nonadditive, selection based on individual performance will be relatively ineffective. For the latter type of trait, the breeding program must be designed to make use of specific crosses that produce favorable gene combinations. This involves crossing lines or breeds to obtain favorable combinations of genes for expressing these traits.

When both types of genetic variation are important, additive for some traits and nonadditive for others, genetic improvement can be maximized by combining selection practiced primarily in purebred herds with systematic crossbreeding practiced in commercial herds. A knowledge of the relative amounts of additive and nonadditive genetic variation that affect each economically important trait is fundamental to the development of effective breeding programs.

FACTORS AFFECTING RATE OF IMPROVEMENT FROM SELECTION

Factors that affect rate of improvement from selection include (1) heritability, (2) selection differential, (3) genetic association among traits, and (4) generation interval.

Heritability

Heritability is the proportion of the differences between animals—measured or observed—that are transmitted to the offspring. Thus, it is the proportion of the total variation caused by additive gene effects. The higher the heritability for any trait, the greater the rate of genetic improvement or effective selection for that trait. When selecting traits of equal economic value, those with high heritability should receive more attention than those with low heritability. Every attempt should be made to subject all animals from which selections are made to as nearly the same environment as possible. This practice will result in a larger proportion of the observed differences among individuals being genetic and will increase the effectiveness of selection. Adjusting for known environmental differences is important before making selections if the environmental factors can be

evaluated. Adjustments can be made for differences in age, age of dam, and sex.

The average heritability estimates for some of the economically important traits of beef cattle are presented in table 1. Of the total difference between the selected individuals and the average of the population from which they were selected, the percentage indicated for each trait is actually transmitted to the offspring. For example, if the selected bulls and heifers were 30 pounds above herd average in weaning weight (selection differential), their progeny would be expected to average 9 pounds heavier than if no selection had been practiced for this trait (30% × 30 = 9).

These heritability estimates were obtained from a large number of research herds under carefully controlled environmental conditions, and adjustments were made for known major environmental sources of variation. The heritability of any trait can be expected to vary slightly in different herds, depending on the genetic variability present and the uniformity of environment. However, estimates from different research herds have been reasonably consistent. The heritability estimates in table 1 probably represent average expectations for many herds, provided the general environment is similar for all cattle within the herd. These estimates indicate that selection should be reasonably effective for most performance traits. However, these traits vary in heritability and economic importance. The rate of their improvement and the emphasis they should receive will also vary considerably.

TABLE 1.—*Heritability estimates of some economically important traits*

Trait	Heritability
	Percent
Calving interval (fertility)	10
Birth weight	40
Weaning weight	30
Cow maternal ability	40
Feedlot gain	45
Pasture gain	30
Efficiency of gain	40
Final feedlot weight	60
Conformation score:	
Weaning	25
Slaughter	40
Carcass traits:	
Carcass grade	40
Ribeye area	70
Tenderness	60
Fat thickness	45
Retail product ......percent..	30
Retail product ....pounds..	65
Susceptibility to cancer eye	30

Selection Differential

Selection differential is the difference between the selected individuals and the average of all animals from which they were selected. Selection differential is determined by the proportion of progeny needed for replacements, the number of traits considered in selection, and the differences that exist among the animals in a herd. If the average weaning weight of a herd is 450 pounds and the individuals retained for breeding average 480 pounds, the selection differential is 30 pounds.

In beef cattle, severe limitations exist on selection differentials pos-

sible for the various traits. The relatively low reproductive rate of beef cattle usually necessitates keeping approximately 40 percent of the females for replacements to maintain the herd and an even higher percentage to expand it. Most of the opportunity for selection is among the bulls because a smaller percentage of the bulls must be saved for replacement. Increasing the number of selection traits reduces the opportunity for selection for any one trait; therefore, selecting only those traits of economic value that are heritable is important. Every effort should be made to obtain the maximum selection differentials possible for the traits of greatest economic importance and of highest heritability, ignoring traits that have little bearing on either efficiency of production or desirability of product.

Genetic Association Among Traits

A genetic correlation among traits is the result of genes favorable for the expression of one trait tending to be either favorable or unfavorable for the expression of another trait. Genetic correlations may be positive or negative. When the association is favorable among traits on which selection is based, the rate of improvement in total merit is increased. Conversely, when a genetic antagonism exists among traits, the rate of improvement from selection is reduced.

Available information indicates a favorable association between rate and efficiency of gain during postweaning growth from 7 to about 18 months of age. A major, unfavorable genetic association that has been reported in beef cattle is a positive genetic correlation between outside fat thickness and marbling score. This means that when marbling (an important determinant of carcass grade) is a selected trait, excessive outside fat also may result. Estimates have been high for genetic correlation between birth weight, preweaning gain, postweaning gain to 12 or 18 months, and eventual mature size. Implications of these and other genetic associations will be discussed in a subsequent section (page 26 to 41) on major performance traits of beef cattle.

Generation Interval

The fourth major factor that influences rate of improvement from selection is the generation interval, that is, the average age of all parents when their progeny are born. Generation interval averages approximately 4½ to 6 years in most beef cattle herds.

The progress made each generation in any trait is equal to the superiority of the selected individuals above the population average from which they came (selection differential) multiplied by the heritability of the trait. This can be put on a yearly basis by dividing by the average length of generation. For example:

$$\text{Annual progress for a trait} = \frac{\text{Heritability} \times \text{Selection differential}}{\text{Generation interval}}$$

When heritability of yearling weight is 50 percent (selected individuals, males and females, are 50 pounds heavier than the average of all animals), and the generation interval is 5 years, then the rate of improvement per year in yearling weight would be $(0.50 \times 50)/5$, or 5 pounds. Progress can be greater when the generation interval is shortened, which can be accomplished by vigorous culling of cows on the basis of production. However, the herd would contain more young or nonproductive-aged cattle.

SELECTION METHODS

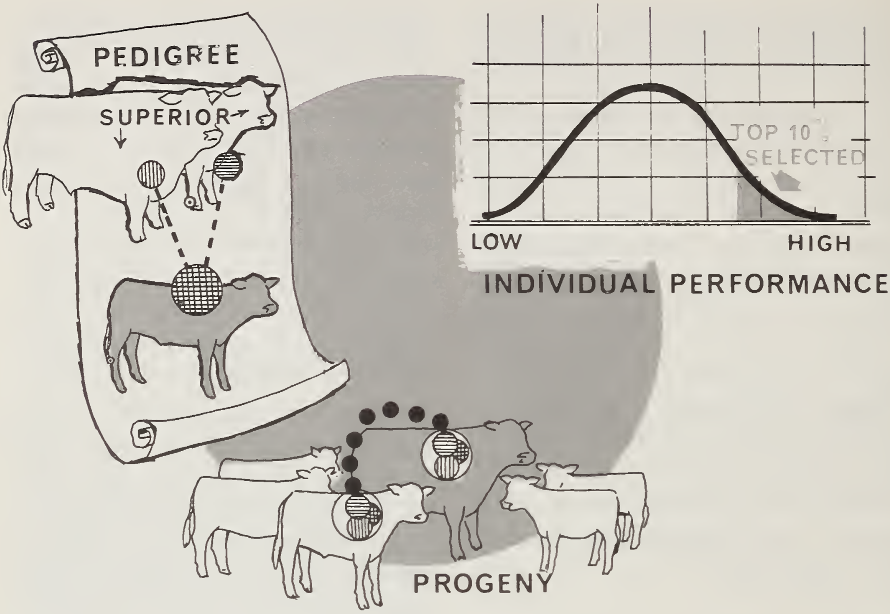
Selection may be based on (1) pedigree, (2) individual performance (mass selection), (3) family performance, (4) progeny test, or (5) a combination of all four.

Pedigree information is most useful in selecting young animals before their own performance or their progeny's performance is known. Pedigree information also may be used in selecting characters that are measured late in life, such as longevity and resistance to cancer eye, or when selecting traits expressed only in one sex, such as mothering or nursing ability (selecting bulls that are progeny of cows that have produced calves with a high average weaning weight). Pedigree information is also useful in selecting against defects such as dwarfism. When pedigree information is used, only the closest relatives should receive much consideration because the most distant relatives can influence the heredity of the individual only through the close relatives (sire and dam). Pedigree information should be given less attention after information on an individual's own performance is available, especially in traits of higher heritability. When information on progeny is available, pedigree information is of less value.

Selection on an individual's own performance (mass selection) will result in rapid improvement when heritabilities are high. An example of such a trait is growth rate. The advantage of selecting on individual performance is that it permits a rapid turnover of generations or shortens the generation interval.

Use of progeny test information results in the most accurate selection when the progeny test is adequate. Progeny tests are needed most in selecting for carcass traits when good indicators are not available in the live animal, for sex-limited traits such as mothering ability when individual performance information is not available on bulls, and for traits with low heritabilities.

The advantage of using progeny test information over pedigree information and individual performance is accuracy, provided the progeny test is extensive. Disadvantages include the less intense culling possible because of the small proportion of animals that can be adequately progeny tested, the longer generation interval required to obtain progeny test information, and



Methods of selection: (1) On the basis of pedigree, or performance of ancestors; (2) on individual performance; and (3) on performance of progeny.

the decreased accuracy as compared with individual performance when not enough progeny are tested or if they are improperly evaluated.

If progeny test information is used, it should be designed so the results can be properly evaluated. The purpose of a progeny test is to obtain the best estimate of the relative genetic merit of the bulls being tested. Therefore, cows must be assigned to the bulls at random. Selection of cows for a particular bull tends to stack the cards either for or against him. Cows should be classified by their age and line of breeding before breeding assignments are made. Cows should then be assigned to breeding groups at random, within line of breeding and age. The sires being progeny tested can then be assigned at random to the different breeding groups. Also important, cows and progeny should be fed and managed uniformly until all the data are obtained. If these precautions are not taken, the progeny test results will be biased, and accuracy of selection can be seriously reduced.

When progeny test information is available, the same data can be used to select between individual progeny by different sires or between members of different half-sib families (half-brothers and half-sisters). Effectiveness of selection based on half-sib family performance depends to a large extent upon the intensity of selection possible, which is determined by the number of families that can be compared. Half-sib

family selection is less accurate than selection based on progeny testing, but it has an advantage of permitting more rapid turnover of generations. This advantage is important for traits that cannot be measured on individuals before they begin reproduction. Thus, half-sib family selection is especially useful for such traits as maternal performance and reproduction.

All four types of information should be used in selecting beef cattle. A good policy is to make initial selections on the basis of pedigree, individual performance, and half-sib family information and to determine the extent a bull or cow is used in a herd in later years based on progeny test information. In traits with high heritability, individual performance should receive nearly all of the emphasis in selection.

ESTIMATED BREEDING VALUE

Breeding value is the animal's value as a breeder determined by the average additive effect of all genes the animal possesses affecting a particular trait. Breeding value is most easily visualized as twice the transmitting ability of an individual, that is, as twice the difference between average performance of a large number of progeny by a sire (or dam) and the population average when the sire (or dam) and other sires (or dams) are mated at random to cows (or bulls) in the population, and all progeny are fed and managed alike. The difference is doubled because parents transmit only a sample one-half (one gene of each pair) of their genes to their offspring.

Breeding value can also be estimated from an individual's own performance relative to the average performance of contemporary animals in the population. The difference between an individual (I) and the average of contemporaries (C), multiplied by heritability (H), estimates breeding value (B), that is, B = H(I-C). Similarly, breeding value of an individual can be estimated on the basis of such information available on relatives as sire or dam and paternal or maternal half-sibs or progeny by also taking into account their relation to the individual and, in the case of half-sibs or progeny, the number of relatives.

Table 2 provides information on the accuracy of selection for each method of selection. Accuracy of selection depends on the correlation between estimated and actual breeding value. A correlation of 1.0 would reflect complete accuracy between estimated breeding value and actual breeding value. Accuracy of selection for each method is determined by the genetic relation between the individual and the relative involved (for example, parent, half-sibs, or progeny), heritability of the trait, and, for half-sib and progeny information, the number of relatives with available unbiased records.

An individual's performance, if available, is always the best single record that can be used to estimate the individual's breeding value be-

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TABLE 2.—*Accuracy and comparative accuracy (relative to individual performance) of selection based on pedigree information, half-sibs, and progeny tests*

Type of relative	Genetic relationship	Number of records	Accuracy[1]			Comparative accuracy[2]		
			Heritability			Heritability		
			0.10[3]	0.30	0.50	0.10	0.30	0.50
Individual	1.00	1	0.32	0.55	0.71	1.00	1.00	1.00
Sire (or dam)	.50	1	.16	.27	.35	.50	.50	.50
Half-sibs (paternal		1	.08	.14	.18	.25	.25	.25
or maternal	.25	2	.11	.19	.24	.35	.34	.33
		4	.15	.25	.30	.48	.45	.43
		10	.23	.34	.38	.71	.61	.54
		20	.29	.39	.43	.92	.72	.61
		40	.36	.43	.46	1.13	.80	.65
		100	.42	.47	.48	1.34	.86	.69
Progeny	.50	1	.16	.27	.35	.50	.50	.50
		2	.22	.37	.47	.70	.68	.67
		4	.30	.50	.60	.96	.90	.85
		6	.36	.57	.68	1.15	1.04	.96
		8	.41	.63	.73	1.30	1.14	1.03
		10	.45	.67	.77	1.43	1.22	1.08
		20	.58	.79	.86	1.84	1.43	1.22
		40	.71	.87	.92	2.25	1.60	1.30
		100	.85	.94	.97	2.68	1.72	1.37

[1] Accuracy is the correlation between estimated and actual breeding value, perfect accuracy = 1.00.

[2] Comparative accuracy is the accuracy of selection based on a particular type of relative expressed as a ratio to individual selection (for example, accuracy of progeny test / accuracy of individual performance).

[3] Levels of heritability are expressed in decimal units, 0.10 corresponds to 10%, 0.20 to 20% and 0.50 to 50%.

cause the genetic relationship is maximal (1.0). A record on the sire or dam is only half as valuable as an individual record because each parent transmits a sample one-half of their genes to the offspring. Therefore, the genetic relationship between parent and offspring is 0.5. The genetic relationship between an individual (for example, sire) and one of his progeny is also 0.5. However, the individual transmits a different sample one-half of his genes to each of his offspring. Therefore, as the number of progeny increases the accuracy of progeny testing increases until with a large number of progeny the correlation between actual breeding value of the sire and estimated breeding value based on average performance of progeny approaches 1.0. The same principle operates to increase accuracy of half-sib family selection as family size increases. However, when the same number of records are available on each type of relative, selection based on half-sibs is only half

as accurate as selection based on progeny tests because the genetic relationship is just half as great (0.25 *versus* 0.50).

Comparative accuracies of each method of selection relative to individual selection (for example, comparative accuracy of progeny test = accuracy of progeny test/accuracy of individual performance) are also shown in table 2. About six progeny are required to make progeny test selection approximately as accurate as individual performance selection at the three levels of heritability. For example, when heritabilities are 0.10, 0.30, and 0.50, progeny test selection with six progeny per sire have comparative accuracies of 1.15, 1.04, and 0.96, respectively, relative to selection based on individual performance information. Selection based on half-sib performance or on progeny tests has greater relative value for traits with low heritability.

Information from all sources including the individual, sire, dam, paternal half-sibs, maternal half-sibs, and progeny, when available, can be combined into a single estimate of breeding value for each animal in a herd. The following information is needed to do this:

(1) An individual's own performance expressed as a deviation or ratio from the average of his contemporaries.

(2) The same as 1, except for the individual's sire or dam.

(3) The average performance of an individual's paternal half-sibs (namely, half-brothers and half-sisters by the same sire) expressed as a difference or ratio from the average performance of all individuals in the herd and the number of half-sibs. The individual's own record should be excluded from the average for the paternal half-sib group.

(4) The same as 3, except for maternal half-sibs (namely, half-brothers and half-sisters by the same dam).

(5) The average performance of an individual's progeny expressed as a deviation or ratio from the average of all contemporaries and the number of progeny.

(6) Heritability of the trait.

(7) The genetic relationship between the individual and different relatives (namely, 0.5 for sire, dam, and progeny and 0.25 for paternal and maternal half-sibs).

This information can be combined into appropriate linear equations that, when solved, provide the best estimate possible of the individual's breeding value. The estimate regresses to average in inverse proportion to the amount of information available to maximize the accuracy of ranking every individual in the herd for breeding value in specific traits. Calculations are complex and difficult to make by hand. Thus, computational details[2] will not be shown, but they can be made quickly by high-speed computers. Performance programs sponsored by breed associations or other beef cattle improvement associations pro-

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[2] Guidelines for uniform beef improvement programs, Extension Service, U.S. Dept. Agr., Program Aid 1020.

vide estimates of breeding value based on individual, sib, and progeny information to their clientele for such specific traits as weaning or yearling weights.

Table 3 provides information on the accuracy of selection for estimated breeding value based on individual performance combined with different kinds and amounts of information that may be available on parents, half-sibs, and progeny. For

TABLE 3.—*Accuracy and comparative accuracy (relative to individual performance) of selection based on estimated breeding value combining information that may be available on parents, half-sibs and progeny*

Type and number of relatives with records						Accuracy[1]			Comparative accuracy[2]		
						Heritability[3]			Heritability		
Individual	Sire	Dam	Paternal half-sibs	Maternal half-sibs	Progeny	0.10	0.30	0.50	0.10	0.30	0.50
1	1	0	0	0	0	0.35	0.58	0.73	1.10	1.06	1.03
1	0	1	0	0	0	.35	.58	.73	1.10	1.06	1.03
1	1	1	0	0	0	.38	.61	.76	1.19	1.12	1.07
1	0	0	10	0	0	.38	.60	.73	1.19	1.09	1.04
1	0	0	20	0	0	.41	.62	.74	1.30	1.12	1.05
1	0	0	40	0	0	.45	.63	.75	1.43	1.15	1.06
1	0	0	0	1	0	.32	.56	.71	1.02	1.02	1.01
1	0	0	0	2	0	.33	.56	.72	1.05	1.03	1.01
1	0	0	0	4	0	.34	.57	.72	1.09	1.05	1.02
1	0	0	0	0	10	.52	.74	.84	1.63	1.36	1.19
1	0	0	0	0	20	.62	.82	.89	1.96	1.50	1.26
1	0	0	0	0	40	.73	.89	.93	2.31	1.62	1.32
1	0	0	0	0	100	.85	.95	.97	2.70	1.73	1.37
1	0	0	20	2	0	.42	.63	.75	1.34	1.15	1.07
1	1	1	20	2	0	.45	.66	.77	1.44	1.21	1.10
1	0	0	20	2	10	.57	.77	.86	1.79	1.41	1.21
1	0	0	20	2	20	.65	.83	.90	2.06	1.52	1.27
1	0	0	20	2	40	.74	.89	.94	2.36	1.63	1.32
1	0	0	20	2	100	.86	.95	.97	2.71	1.73	1.37
1	1	1	20	2	10	.58	.78	.86	1.84	1.42	1.22
1	1	1	20	2	20	.66	.84	.90	2.09	1.53	1.28
1	1	1	20	2	40	.75	.90	.94	2.37	1.63	1.33
1	1	1	20	2	100	.86	.95	.97	2.72	1.73	1.37

[1] Accuracy is the correlation between estimated and actual breeding value, perfect accuracy = 1.00.

[2] Comparative accuracy is the accuracy of selection based on a particular type of relative expressed as a ratio to individual selection (for example, accuracy of progeny test / accuracy of individual performance).

[3] Levels of heritability are expressed in decimal units, 0.10 corresponds to 10%, 0.20 to 20% and 0.50 to 50%.

traits that are highly heritable (for example, 0.50), information on the sire, dam, or maternal half-sibs adds little to the accuracy of selection. Information on a large number of paternal half-sibs helps only a little, but information on progeny increases accuracy of selection substantially even for highly heritable traits.

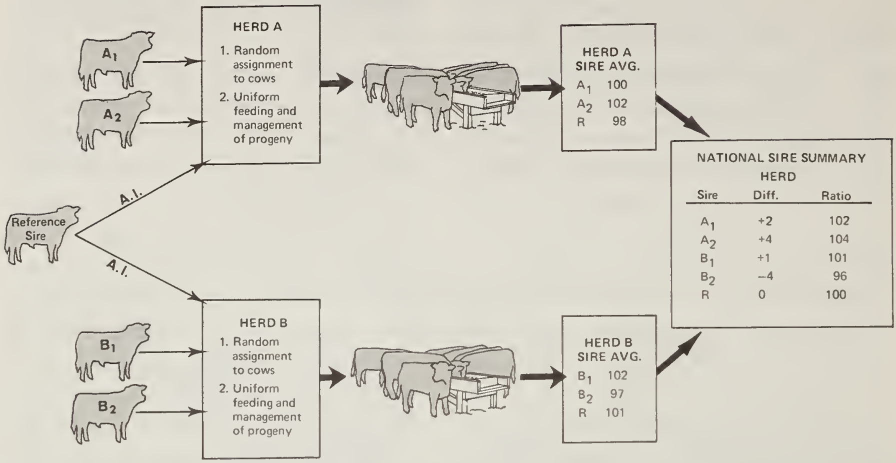
Estimates of breeding value based on all sources of information are really most useful relative to individual selection for traits with a low heritability. When heritability is low (for example, 0.10), progeny information is again the most valuable source of information that can be added to that of the individual. However, when progeny information is not available, paternal and maternal half-sib data or even information on the sire and dam can effectively contribute to increased accuracy of selection for traits of low heritability. Use of estimated breeding value based on all available information should be encouraged as an appropriate selection criterion especially for traits with a low heritability.

Reproduction traits have low heritability. Efforts have only recently been made to incorporate measures of reproduction into performance records programs. As records on fertility traits become available, effectiveness of selection for fertility can be enhanced by use of estimated breeding value. Their use will be most effective in herds using a large number of sires to produce a large number of paternal half-sib families.

NATIONAL SIRE EVALUATION

In recent years progeny testing has been extended to provide for evaluation of sires used in different herds. This was not possible in beef cattle for many years because artificial insemination was used to only a limited extent. Progeny tests conducted within herds provided for good estimates of differences in transmitting ability between bulls used at the same time in the same herd; however, to compare bulls used in different herds was not possible because the progeny had different sires and were out of different cows and raised in different environments for each herd. To overcome this difficulty, a number of breed associations have developed national sire evaluation programs following guidelines[2] of the Beef Improvement Federation. The guidelines are based on widespread use in different herds of certain bulls designated as reference sires. When reference sires are used in several herds through artificial insemination, comparisons can be made between sires through the tie provided by the reference sires common to each herd.

Results are reported in terms of expected progeny difference for traits of economic importance. The expected progeny difference estimates the transmitting ability of sires evaluated in the program. Because each sire transmits one-half of his heredity to each offspring, the expected progeny difference estimates one-half of the sire's breeding value. The expected progeny difference re-



National Sire Evaluation is possible by comparison to reference sires used through artificial insemination in different herds.

gresses to the average in inverse proportion to the number of progeny produced by the sire to maximize the accuracy of evaluation. Thus, the expected progeny difference provides the most accurate estimate available on how future progeny by various sires evaluated are expected to perform relative to the set of reference sires used in the breed.

Results of the sire evaluation program are generally published in a National Sire Summary. Effectiveness of selection and rate of genetic improvement in the breed can be enhanced when the outstanding sires are used extensively through artificial insemination or when the information is used as a paternal half-sib test to select outstanding sons of bulls that rank well in the National Sire Summary.

TYPES OF SELECTION

The three types of selection are (1) tandem selection, (2) selection based on independent culling levels, and (3) selection based on an index of net merit.

Tandem is selection for one trait at a time. When the desired level of performance is reached in this trait, a second trait is given primary emphasis, and so forth. This is the least effective of the three types and is not recommended. Its major disadvantage is that, by selecting for only one trait at a time, some animals extremely poor in other traits will be retained as replacements.

Selection based on independent culling levels requires that specific levels of performance be attained in each trait before an animal is kept for replacement. This is the second most effective type of selection. It has this disadvantage: in requiring

specific levels of performance in all traits, it does not allow for slightly substandard performance in one trait to be offset by superior performance in another.

Selection based on an index of net merit gives weight to the traits in proportion to their relative economic importance and their heritability and takes cognizance of the genetic association (if any) among the traits. This is the most effective type of selection, because it allows slightly substandard performance in one trait to be offset by outstanding performance in another. By giving additional weight to traits of higher heritability or greater economic importance, greater improvement in net merit can be attained.

The use of the index or some modification of it is the preferred type for most herds.

The larger the number of traits selected, the slower the progress in any one of them; hence, giving major consideration only to traits of economic value that have reasonably high heritabilities is desired. The reason differences in heritability of traits should be considered is that the opportunity for selection should be used on traits that will respond. Obviously, if a trait has extremely low heritability, little genetic improvement in it can be expected. When such a trait is given attention, the emphasis that can be put on traits that give a greater response to selection (higher heritability) is reduced.

Although traits of little or no economic importance or of low heritability should be given little or no attention in selection, all heritable traits of economic value should be considered concurrently. The attention they receive should be determined by their relative economic value and their heritability.

Although increasing the number of traits reduces the selection differential for any one trait, it results in more rapid improvement in total genetic merit or net worth. Average reduction in progress in each trait after considering several traits is approximately $1/\sqrt{n}$, where n is the number of traits selected for. For example, if four genetically independent traits are involved in selection, the selection differential for each of them will be approximately half when only one trait is involved ($1/\sqrt{4} = \frac{1}{2}$). This is based on the assumption that no genetic associations (either favorable or unfavorable) exist among the four traits. Considering all heritable, economically important traits simultaneously will result in more rapid improvement in genetic merit involving all traits.

Relative rates of improvement in some traits of economic value with different selection intensities or different percentages saved for breeding are considered in table 4. These estimates are based on phenotypic evaluation for the traits indicated and assume that the percentage saved and used produce progeny that have an opportunity to be selected for the next generation. For example, the selected bulls from each generation are sired by bulls selected

TABLE 4.—*Estimates of potential progress in 10 years when different intensities of mass selection are practiced for specific traits*[1]

Trait	Percentage of bulls saved					Assumptions[1]
	1	10	20	50	70	
Weaning weight and						
No other traits ....pounds..	41.6	30.6	26.4	19.2	15.6	50 percent of heifers saved; h^2, 0.3 in both sexes;[2] SD, 40 lb. in both sexes.[3]
1 other trait ....do....	29.4	21.6	18.7	13.6	11.0	
2 other traits ....do....	24.0	17.7	15.2	11.1	9.0	
3 other traits ....do....	20.8	15.3	13.2	9.6	7.8	
Postweaning daily gains and						
No other traits ....do....	.44	.30	.25	.17	.12	50 percent of heifers saved; h^2, 0.5 in bulls, 0.3 in heifers; SD, 0.29 lb. in bulls, 0.20 lb. in heifers.
1 other trait ....do....	.31	.21	.18	.12	.08	
2 other traits ....do....	.25	.17	.14	.10	.07	
3 other traits ....do....	.22	.15	.12	.08	.06	
Yearling weight and						
No other traits ....do....	147.4	103.2	86.4	57.6	43.2	50 percent of heifers saved; h^2, 0.6 in bulls, 0.4 in heifers; SD, 80 lb. in bulls, 60 lb. in heifers.
1 other trait ....do....	104.2	73.0	61.1	40.7	30.5	
2 other traits ....do....	85.0	59.5	49.8	33.2	24.9	
3 other traits ....do....	73.7	51.6	43.2	28.8	21.6	
Yearling conformation score and						
No other traits ....units...	1.39	1.02	.88	.64	.52	50 percent of heifers saved; h^2, 0.4 in both sexes; SD, 1 unit in both sexes.
1 other trait ....do....	.98	.72	.62	.45	.37	
2 other traits ....do....	.80	.59	.51	.37	.30	
3 other traits ....do....	.70	.51	.44	.32	.26	

[1] Assumes that selection is only for the criteria indicated and when selection is for more than 1 trait, each trait, is given equal emphasis and that the traits are inherited independently. Generation interval, 5 years.

[2] h^2, heritability.

[3] SD, standard deviation—an estimate of variation.

by the same criteria in the previous generation. Table 4 shows the advantages of saving bulls from among the top and of selecting only for traits that have real economic value. Obviously, a closed-herd system must be used for the above conditions to prevail.

MATING SYSTEMS

The five fundamental types of mating systems are (1) random mating, (2) inbreeding, (3) outbreeding, (4) assortative mating, and (5) disassortative mating.

(1) Random mating is mating individuals without regard to similarity of pedigree or similarity of performance (phenotype).

(2) Inbreeding is mating individuals that are more closely related than the average of the breed or population. Linebreeding is a special form of inbreeding and refers to the mating of individuals so the relationship to a particular individual is either maintained or increased. This method automatically results in some inbreeding because related individuals must be mated to accomplish linebreeding.

(3) Outbreeding is mating of individuals that are less closely related than the average of the breed or population. The term "outcrossing" is also used to mean outbreeding when matings are made within a breed. Crossbreeding is a form of outbreeding.

(4) Phenotypic assortative mating is the mating of individuals that are more alike in performance traits (phenotype) than the average of the herd or group. Phenotype refers to individual performance in all traits that can be measured in an individual.

(5) Phenotypic disassortative mating is the mating of individuals that are less alike in performance traits (phenotype) than the average of the herd or group.

Inbreeding and outbreeding refer to similarity of pedigree or relationship, and phenotypic assortative and disassortative mating refer to phenotypic resemblance (likeness in performance traits).

Inbreeding sometimes affects performance traits or results in some reduction in general vigor. However, herds of reasonable size, where several sires are used, can be maintained closed to outside breeding for long periods without any increase in inbreeding or decline in performance associated with inbreeding.

Within a closed herd where the mating is random as far as relationship is concerned, the rate of increase in inbreeding per generation is $1/8m + 1/8f$, where m is the total number of males used in each generation and f is the total number of females in the herd in each generation. Thus, in a 100-cow herd where four sires are used for each generation with 100 cows in the herd for each generation, the inbreeding increase for each generation is $1/8(4) + 1/8(100) = 1/32 + 1/800 = 0.031 + 0.0012 = 0.0322$ or 3.22 percent per generation. When generation interval is 5 years, 15 years on such a program would result in a herd

with average inbreeding of 9.66 percent. This is not a rapid rate of inbreeding. For example, the mating of half-brothers and half-sisters results in offspring that are 12.5-percent inbred. Offspring of sire-daughter, son-dam, and full brother and sister matings are 25-percent inbred.

Sire numbers for each generation are of paramount importance in affecting rate of inbreeding. The rate of inbreeding can be reduced by deliberately avoiding close matings such as sire-daughter and half brother and sister. Linebreeding may result in some loss of vigor, but if the animal to which a herd is being linebred is one of truly outstanding merit, the increase in performance as a result of intensifying the genes of an outstanding individual may more than offset any decline in performance caused by inbreeding. Rigid selection accompanying linebreeding should be effective in reducing some of the undesirable effects of inbreeding. When inbred or linebred herds are outcrossed, the loss of vigor that accompanies inbreeding is restored.

Linebreeding and inbreeding make the individuals in a herd more alike genetically and thus more uniform in their transmitting ability. A major advantage of linebreeding and inbreeding is that a breeder knows his own herd better than he knows someone else's; thus, he is likely to do a more effective job of selecting from within his herd.

The effectiveness of linebreeding depends primarily on the genetic merit of the animal to which the linebreeding is directed.

Many breeders fear the consequences of inbreeding. Inbreeding intensifies what is already present in the herd, including poor traits as well as good. If an undesirable trait is present in the herd, inbreeding tends to bring it to light. However, inbreeding is not the cause, as the genes responsible for the undesirable effect were already present. For example, if genes responsible for undesirable traits such as dwarfism are present in a population, inbreeding may increase the number of dwarf calves born, but it is not the cause of dwarfism.

Inbreeding may be used to evaluate the presence of undesirable genes in a herd. If accompanied by rigid selection, it may be effective in reducing the frequency of them.

The disadvantages of linebreeding and inbreeding are that the foundation animals may not be truly superior. A genetic defect in the foundation animals can by chance rise to a high frequency and greatly interfere with the breeding program and materially reduce the value of the herd regardless of its genetic merit for major performance traits. Because it reduces genetic variation, inbreeding results in decreased heritabilities and selection on individual performance is less effective. Because inbreeding makes individuals more alike in their genetic makeup, it increases the effectiveness of family selection.

In summary, linebreeding and inbreeding should be practiced only in

herds of outstanding genetic merit. The herds should be large enough so the rate of inbreeding will be slow enough to provide opportunity for selection before genetic variation is reduced to the point where selection is ineffective. All commercial producers and purebred breeders with small herds or herds of average genetic merit should avoid linebreeding and inbreeding.

Outbreeding or outcrossing is recommended for all commercial producers and for secondary seedstock herds. That is, close mating should be avoided. However, owners of secondary seedstock herds may profitably obtain bulls from linebred herds. When sources of linebred bulls are changed periodically for use in secondary herds, the system is still outbreeding. When outcrossing linebred herds to correct a deficiency becomes necessary, breeders may find outcrossing advantageous to other linebred herds that are particularly outstanding in the trait that needs improvement. After such an outcross, resuming a program of linebreeding may be desirable.

Many breeders practice assortative and disassortative mating. Assortative mating includes mating superior cows to superior bulls or mating poorer cows to unproved or less highly regarded sires. Disassortative mating is practiced when a breeder is attempting to make "corrective matings." That is, he may mate cows that are mediocre or poor in one trait to bulls he considers superior or outstanding in that trait. Assortative mating results in increased variation in a herd; disassortative mating reduces the genetic variation in a herd.

USE OF RECORDS

Traits of economic value are commonly referred to as performance traits. These traits contribute to efficiency of production and desirability of product. A performance record is the systematic measurement of traits of economic value and the use of these records in selection. Performance records help breeders find animals that are genetically superior in all economically important breeding traits.

Any system of measurements makes possible the evaluation of differences between animals. Preferred measurements are those that give the most accurate estimate of the breeding value or genetic merit of an animal relative to others in a herd. Records increase a breeder's knowledge of differences between animals and thus increase the accuracy of his selections.

Research on beef cattle breeding shows that appreciable genetic improvement can be made in most traits of economic value by selection on the basis of differences in individual performance (table 2). Such research involves methods of measuring these traits and estimating their heritability and developing selection procedures for traits that contribute to both productive efficiency and carcass merit.

Performance records of animals should be adjusted to eliminate

Performance records provide a basis for selecting genetically superior animals.

known environmental differences so genetic differences will be a larger part of the total differences measured or observed. Adjustments should be made for differences in age, sex, age of dam, and other environmental variables that can be measured or evaluated. Because any increase in environmental variation obscures genetic differences and decreases the effectiveness of selection, every precaution should be taken to measure economically important traits as accurately as possible. For example, an effort should be made to equalize fill in animals before they are weighed because errors in weighing decrease the accuracy of selection. Fill can be equalized somewhat by removing water and feed for 12 hours before weighing and by recording more than one weight. This applies to both initial and final weights.

Performance records are useful primarily to compare cattle handled alike within a herd but not to compare differences between herds. Such large environmental differences as location, management, and nutrition are likely to exist between herds. Adjusting accurately for these differences is difficult. Genetic differences between herds do exist, but large environmental differences make the evaluation of genetic differences difficult.

Average weaning weights of 500 pounds may be realistic in some environments and in some production programs; whereas, 350-pound weaning weights may be reasonable under more adverse conditions. Yet, beef cattle may provide the most desirable means for land use under both conditions. Furthermore, the genetic merit of a herd weaning 350-pound calves may be equal or even

superior to that of a herd weaning 500-pound calves. Standards of performance expressed as deviations from individual herd or group averages are advisable for making within-herd comparisons. Comparisons between herds based on minimum standards of performance can be undesirable and misleading.

Minimum performance standards for production and carcass traits have been considered in some performance record programs. Because of the variation in environmental conditions and production programs, standards involving between-herd comparisons may give preference to herds carried under superior environmental conditions rather than those that are genetically superior.

Comparison of animals within a herd that are subject to different environmental conditions, such as having part of the calves on nurse cows, is as objectionable as comparison of records from different herds. When variations in treatments exist, comparisons should be restricted to animals treated alike, unless appropriate adjustments can be made for treatment effects.

All economically important traits that are heritable should be evaluated for all animals in a herd. An effective performance record program should be compatible with practical management regimes. Cattle should be evaluated under similar environmental conditions in which their progeny are expected to perform.

From the standpoint of genetic improvement for the entire beef cattle industry, performance records will have greatest impact in purebred or seedstock herds. Commercial producers can use performance records to cull cows, to select replacement heifers, and to evaluate bulls on their progeny's performance where progeny groups are kept under comparable conditions. Because approximately 40 percent of all heifers must be saved for replacements just to maintain a herd, selection opportunities among females are limited. Commercial producers can also make effective use of performance records by selecting bulls from purebred or seedstock herds that are on a systematic performance record program. In selecting herd bulls from their own herds as well as from other breeders' herds, purebred breeders should evaluate their records as compared with the herd average. The inherent productivity of any herd depends largely on the genetic merit of the bulls used.

The goals in performance records are not greatly different from those that have always been sought by progressive breeders. The principal differences lie in a systematic recordkeeping program and the use of these records in making selections. Performance records up to slaughter require no new or additional facilities except a scale and forms for keeping records.

Features of a good performance record program are as follows:

1. Give all animals equal opportunity.

2. Keep systematic, written rec-

ords of all economic traits on all animals.

3. Adjust all records for such known sources of variation as age of dam, age of calf, and sex.

4. Maintain records for selecting replacement stock and for culling poor producers.

5. Keep nutritional program and managment practices practical and compatible with those where progeny of the herd are expected to perform and are uniform for the entire herd.

No effort has been made in this publication to provide guidance for an individual performance record program. Methods differ in different areas, and breeders are advised to adopt methods used in their areas or sponsored by their breed association.

Relative emphasis put on the different traits may vary in different herds, but the attention that each trait receives should be based primarily on its heritability and economic importance to the entire beef cattle indusry. Keeping records does not change what an animal will transmit; records are used to locate the genetically superior individuals. If genetic improvement is to be accomplished, the superior animals must be selected.

MAJOR PERFORMANCE TRAITS

All traits of economic value should be considered in selecting beef cattle. The major traits influencing productive efficiency of highly desirable beef are (1) reproductive performance, or fertility, (2) mothering or nursing ability, (3) rate of gain, (4) efficiency of gain, (5) longevity, and (6) carcass merit.

Maximum production efficiency is not necessarily related to maximum performance levels in all of these traits. For example, maximum milk production and larger cow size associated with rapid growth rate are not desirable when feed supply for cows is limited because reproduction is adversely affected.

Additional nutrient requirements for lactation and maintenance may not be met. Thus, with the possible exception of reproduction, emphasizing the same criteria of selection within all breeds is not desirable for use in all production situations.

Fertility

A high level of fertility or reproductive performance is basic to an efficient beef cattle industry because the percentage of the total beef cattle population composed of cows is high, requiring a major portion of the resources used in beef production. No single factor in commercial cow-calf operations has greater bearing on production costs than percentage calf crop. Also, a high level of reproduction is fundamental for making genetic improvement. A high calf crop decreases the percentage that must be saved for replacement and thus increases the selection differential possible for other traits. Both the male and female should be considered in selecting for reproduction; reduced calf crops can result from reduced fertility of either.

Fertility is a complex trait. A live calf at weaning is the product of a long sequence of events, each of which must succeed, from the time a cow is turned with a bull until her calf is weaned. The bull must have a high degree of libido and be physically capable of mating and producing enough viable sperm to maximize fertilization. The female must reach puberty as a heifer, or have a sufficiently early calf and short postpartum as a cow, to exhibit a fertile estrus during the breeding season. Ovulation, implantation, embryonic and fetal development, and parturition must occur without failure. The calf must consume colostrum and milk vital for early survival and to ward off other hazards before weaning. With such a long chain of events involving interrelationships between the sire, dam and offspring and their environment, the probability that any one event can succeed can be high and still the probability that the product of all events will succeed (percentage calf crop weaned) can be somewhat low. A breakdown at any point in the sequence can be devastating.

Variation in reproduction is large. For example, percentage calf crop can easily range from 75 to 90 percent even among large herds. Results indicate that heritability of such traits as calf crop, pregnancy rate, and calving interval is low (10 percent). Therefore, most of the variation may not be caused by additive genetic differences between herds but rather by differences in management, nutrition, herd health, and other environmental factors or by nonadditive genetic differences (for example, heterosis) and interactions between genotype and environment. So many random, or chance, environmental factors affect fertility from the time a cow is turned with a bull until her calf is weaned that fertility in any given year reveals little of the real genetic differences among cows. Better measures of fertility are needed for cows and bulls. There are indications that certain components of fertility such as age at puberty and first service conception rate in heifers are more highly heritable than calf crop percentage.

When heritability of fertility is low, detailed records should be kept on reproductive traits. Records on reproduction are useful in identifying management problems that can be modified to improve reproductive performance in the herd. Even with low heritability, rigid culling to remove open cows or problem breeders can be useful in bringing about a more profitable reproductive pattern in a herd. Instances are reported where close culling for fertility has improved calf crop. Environmental effects influencing such traits as early calving date tend to have a permanent influence on reproduction in subsequent years. Most of the improvement is not additively genetic, that is, if the practice were discontinued, reproduction would decline in subsequent generations. However, selection pressure on reproduction is not wasted because reproduction is of overwhelming economic importance. The return from

culling open and other problem cows and keeping pregnant cows increases the number of calves weaned relative to cost of production and does provide greater opportunity to select for other economically important traits because of a larger total number of offspring available.

In herds where reduced calf crops are a problem, close attention to feeding, disease control, and management practices is definitely indicated. Reproductive diseases markedly influence fertility. Level of feeding is important, particularly level of energy, vitamin A, protein, and phosphorous. Many breeders and commercial producers can profitably give attention to these items in increasing calf crop.

Calving Difficulty and Birth Weight

A high degree of calving difficulty cannot be tolerated in commercial beef production. Not only is the expense of labor for assistance at calving a prohibitive factor, but calving difficulty can cut deeply into calf crop weaned by reducing calf survival and postpartum conception in cows. For example, at the U.S. Meat Animal Research Center, calf mortality was four times greater in calves experiencing difficult births (assistance given with a calf puller or Caesarean birth) than in those not experiencing difficult births (20 percent *versus* 5 percent). Conception rate in the next breeding season was 16 percent lower in cows requiring assistance at calving than in those requiring no assistance. Cow age and calf birth weight are two of the most important factors influencing calving difficulty. One study showed that, regardless of cow age, calving difficulty increased 1 percent for each pound increase in calf birth weight. However, the association between calving difficulty and birth weight was strongest in 2-year-old first calf heifers, reduced but still strong in 3-year-olds, and much lower in 4- and 5-year-old cows experiencing a low incidence of calving difficulty.

Pelvic size and other physical measures of cows and calves have been shown to be associated with calving difficulty, but these factors have also been associated with calf birth weight. Their association, independent of age and birth weight, has been too low to accurately predict calving difficulty or serve as an appropriate selection criterion for calving ease. Apparently, selection of heifers with larger pelvic area will result in females with larger pelvic area, but they will also be larger in size generally and will produce calves with proportionately heavier birth weights. Thus, the net effect of selection for pelvic area on calving difficulty may be quite small.

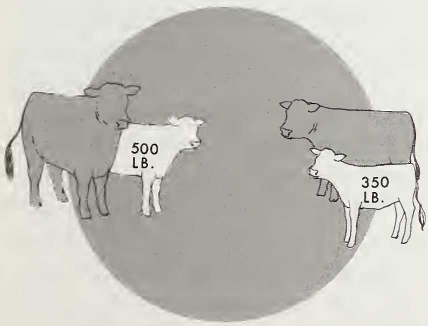
Selection for smaller birth weight appears to be the most effective criterion for improving calving ease because it is the best single indicator of calving difficulty. For calving ease, birth weight may be a more sufficient selection criterion than calving difficulty because it can be measured more accurately and ob-

jectively on calves from cows of all ages. Calving difficulty is generally expressed to a high degree only in first- and second-calf females. Birth weight is affected by sex of calf and increases with advancing cow age. Thus, adjusting birth weight is necessary for sex of calf and age of dam. This can be done by expressing birth weight as a ratio to sex-age of dam-management group averages.

Nursing or Mothering Ability

The ability of a cow to wean a healthy, vigorous calf is vital to efficient beef production. In the broadest sense, reproduction, calving ease, livability, maternal behavior, and milk production are all important components of mothering ability.

Increasing pounds of calf weaned per cow exposed to breeding can increase efficiency of production because such fixed costs as veterinary, labor, and bull service are on a per head basis of the total herd. Feed costs per cow seem closely related to size of cow and level of milk production, but faster gains of calves decrease feed requirements of calves per unit of gain and heavier weights at weaning reduce the amount of feed and time required for calves to reach a desired final slaughter weight. This takes on increasing importance if feed grains increase in price relative to other feed resources used by cows. Thus, increased weaning weight from increased milk production can be efficient when cows are converting economical low-quality feedstuffs into milk—a high quality source of protein and energy—that can be used efficiently by the calf supplementary to that available from forages.



The ability to wean heavy, vigorous calves is an important economic trait that can be improved by selection.

Milk yield, perhaps more than any other trait, must be synchronized or matched with feed resources available to maximize efficiency of production. Optimum milk yield is neither maximum nor minimum milk yield in most situations.

Increased milk yield increases weaning weight per calf, but increased weaning weight per calf from milk yield can be detrimental if weaning weight per cow is reduced as a result of impaired rebreeding performance. Rebreeding performance of cows can be reduced through longer postpartum intervals and reduced conception in cows producing high levels of milk when nutrient requirements are not met to provide for increased milk production and maintenance of body weight.

On the other hand, milk produc-

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tion can be too low. Milk production can be so low that survival and ability of calves to combat disease, parasites, and other environmental hazards can be reduced. When weaning weights of calves are low and calves are unthrifty, selection for improved nursing ability is indicated provided other health and disease considerations have been ruled out.

Weaning weight of the calf is used as a measure of nursing ability. The calf's genetic impulse for growth is confounded with nursing ability by this procedure. However, this is not a serious handicap because half the growth impulse of the calf is transmitted by the dam.

Selection of bulls and replacement heifers that have heavy weaning weights relative to the herd average will lead to genetic improvement in nursing ability. In selecting for increased weaning weight, the breeder often selects for mothering ability, as well as for the calf's own ability to grow. However, research information indicates that selection among cows for mothering ability should be reasonably effective. This can be accomplished by selecting cows on the basis of the weaning weights of their calves; cows that wean calves heavier than the herd average in one year are more apt to produce calves heavier than average in succeeding years.

Differences in mothering ability can be evaluated about as accurately on the basis of 112-day calf weights as on the conventional weaning age of approximately 205 days. If calves are creep-fed, 112-day calf weights are perhaps preferable. Adjustment for differences in age of dam, sex of calf, and age of calf is necessary because these factors influence weaning weight. In adjusting for differences in calf ages, average daily gain from birth to weaning should be used for each calf (subtract actual birth weight, calculate average daily gain, and adjust to standard age for the group).

Mothering ability of cows may be compared within groups of the same sex of calf and of similar age of cows if numbers are large. This avoids an adjustment for differences in sex of calf and age of dam. The most accurate adjustment factors for sex of calf and age of dam are those developed in the herd in which they are used, provided the data are not biased by selection or management differences and the herd is large enough for reliable estimates to be made. Adjustment factors for smaller herds should be developed from herds with similar management regimes. Records are more accurate where the calving season is relatively restricted so that major differences in age and seasonal influences are avoided. Because weaning weight is used as a measure of mothering ability, all calves should be treated the same (such as creep-feeding all or none) so that the major variable is difference in nursing ability of the cows.

Indications are that selection for yearling weight may put as much pressure on nursing ability as selection for weaning weight. It has been observed repeatedly that the effect

of age of dam on final weight is essentially the same as on weaning weight and that effects of age of dam on postweaning gain are negligible. This indicates that differences in preweaning gain associated with maternal environment are not compensated for in the subsequent postweaning period.

Selection of heifers on the basis of heavy weaning weight to increase nursing ability is less effective than selection of bulls with outstanding weaning weights. Results from several experiments have shown that heifers raised by cows providing a superior maternal environment may in turn provide a poorer maternal environment for their progeny than would be expected based on their own weight. The relationship for weaning weights has been greater between offspring and grand dam than between offspring and dam even though their genetic relationship is only half as large (1/4 *versus* 1/2).

Studies of effects of age of dam on weaning weight and on subsequent nursing ability of females have helped to clarify these relationships. Heifer calves raised by young cows (2- or 3-year-olds) or by older cows (10 years old or older) have lighter weaning weights than those raised by mature cows (5 to 9 years of age). However, heifers raised by young or old cows have been superior in nursing ability to those raised by mature cows. Thus, a superior maternal environment promoting a heavier weaning weight of a heifer calf can have a permanent negative effect on her performance as a cow.

The negative influence of a superior maternal environment may be caused by additional fat deposition in heifers raised by mature cows compared to those raised by young cows associated with greater milk production of mature cows. The possibility exists that fat deposition interacts with subsequent mammary and udder development in the growing female to reduce subsequent milk production; however, other mechanisms may also be involved. Whatever the underlying biological mechanism, results indicate that if increased nursing ability is a selection objective, progress may be increased by selecting heifer replacements from the youngest heifers in the herd. Although selection intensity will be reduced when only heifers from the youngest cows are considered for prospective replacement, the generation interval will be shortened and progress will be made if intense sire selection for weaning weight is practiced and cows with the poorest maternal performance are culled.

Growth Rate

Growth rate is important because of its high association with economy of gain and its relation to fixed costs —veterinary, buildings, grazing fees, labor—that are on a per-head or per-unit-of-time basis. In most instances differences in growth rate have been measured in time-constant, postweaning feeding tests, and

results indicate that differences in growth rate can be appraised rather accurately in this manner. A postweaning period of at least 140 days is required to measure differences in growth rate. This minimum length is based on rather uniform initial weights, condition, age, and previous treatments. Final weight at 12 to 18 months (standardized for age differences) is a more highly heritable measure of differences in growth rate than any individual component of final weight (that is, birth weight, preweaning gains, and postweaning gains).

Final weight at a standard age of 18 months fits the management programs of many purebred herds. Bulls born in the spring can be carried on a low level of concentrate feeding (4 to 5 pounds of concentrates plus full feed of roughage) their first winter and fed at a higher level of concentrate, either on grass or in drylot, during their yearling summer. By this procedure bulls are developed at a high enough level of feeding and over a long enough period for genetic differences in growth rate to be expressed, and a good appraisal of growth can be made. Bulls handled in this manner are in good sale condition at a desirable age and season. Postweaning gains are measured for approximately 345 days, and gains made in this period can be added to 205-day weaning weight, appropriately adjusted for age of dam, to arrive at an adjusted 550-day weight.

Final weight and grade at somewhere near normal market age for a high percentage of slaughter cattle seems to be of most interest on an industrywide basis. The use of postweaning gain alone as a measure of growth could foster poor milking ability because of compensatory gains. A poor feed supply in one period tends to be followed by a period of increased rate of gain.

An alternate program for measuring growth rate in bulls is to feed at a higher level and for a shorter period immediately after weaning. Bulls may be put on feed when they are weaned and full-fed for 5 to 6 months on a ration of approximately equal parts of concentrates and roughage to two parts concentrates and one part roughage. In this program an adjusted final weight at 365 days can be used as a measure of differences in growth rate. For example, adjusted 365-day weight may be obtained by adding the gain made in a 160-day postweaning period to 205-day weaning weight, appropriately adjusted for age of dam. The postweaning feeding pe-

Adjusted yearling weight is an important economic trait that can be improved by selection.

riod may be intermediate to the two described above—for example, it may be 247 days with an adjusted final weight of 452 days computed and used as a basis for selection.

Research results indicate that a reasonably high level of feeding is desirable to appraise differences in growth rate most accurately. If a lower level of feeding is used, the period for measuring differences in growth rate should be longer. However, a relatively low level of feeding, promoting gains of 1 to 1.25 pounds per day, is recommended for heifers during their first winter. Gains of 1 to 1.25 pounds per day are adequate in most breeds to promote early sexual maturity so that the heifers can be bred at 13 to 14 months to calve as 2-year-olds. Research results indicate that full-feeding a high-concentrate ration during the first winter may interfere with reproductive performance and mothering ability. Because a high percentage of heifers must be kept for replacements, little opportunity exists to select among heifers for differences in growth rate. Hence, from this standpoint, little can be gained from the heavy feeding of heifers.

When selecting heifer replacements for differences in growth rate, long yearling age (approximately 18 months) should be used, with adjustments in the same manner suggested for bulls (by adding the gain made after weaning to weaning weight, adjusted to a constant age, and appropriately adjusted for age of dam). This assumes that heifers are carried at a relatively low level of feeding during their first winter. If heifers are bred as yearlings, to make selections before 15 months of age may be desirable. This can be done effectively with a 247-day postweaning period and adjusting final weight to 452 days.

Genetic correlations among measures of growth or size at different ages (for example, birth weight, weaning weight, 12- or 18-month weight, and mature weight) are high. Genetic correlations among these traits are higher than phenotypic correlations. Thus, 12- or 18-month weight is more highly heritable than any of its components (namely, birth weight, preweaning gain, and postweaning gain). However, other consequences are that selection of 12- or 18-month weight leads to significant increases in birth weight and mature size. Increases in birth weight contribute to increased calving difficulty associated with reduced survival of calves and reduced rebreeding performance of dams. Increases in mature weight of cows increase nutrient requirements for maintenance of the cow herd, which at least partially offsets the advantages of more rapid and efficient gains of the progeny slaughtered.

Hence, recent studies have been conducted to evaluate genetic variation in shape of the growth curve, to assess the feasibility of increasing weights at market ages while minimizing changes in weight at birth and maturity. Results from several studies have been encouraging. For example, degree of maturity (ratio

of immature weight to mature weight) at weaning or yearling ages is moderately to highly heritable (40 to 50 percent). However, degree of maturity is not an effective selection criterion because it requires measurement of weight at maturity, which comes too late in life for effective selection to be practiced. Thus, some research has been conducted to evaluate alternative selection criteria involving functions or indexes of immature weights that may be favorably related to degree of maturity for weight at market ages.

Encouraging results were reported in a study of selection criteria for efficient beef production with net effects of calf mortality, reproduction, and cow size included in the definition of economic efficiency. Results indicated that selection for heavier yearling weight (Y) but lighter birth weight (B) with an index = Y-3.2B would increase improvement in efficiency 6 to 7 percent more than selection for yearling weight alone. Adding this degree of selection against birth weight reduced expected increases by 55 percent in birth weight and by 25 percent in mature weight but only by 10 percent in yearling weight.

Other results have indicated that selection for postnatal relative growth rate (RGR) would have a similarly favorable effect on shape of growth curve reducing response in birth weight and mature weight relatively more than weight at market ages. Relative growth rate was measured as

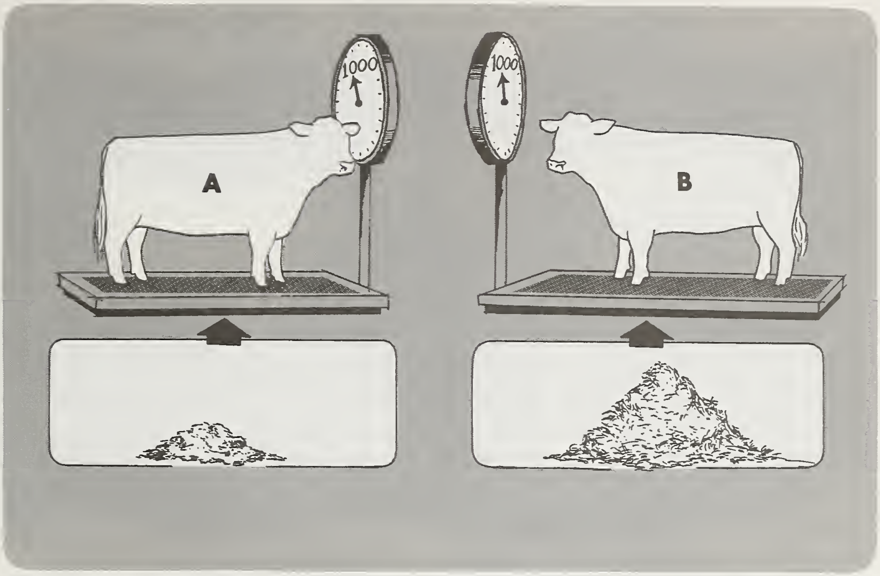
$$RGR = \frac{1nW_{t2} - 1n\ W_{t1}}{t_2 - t_1},$$

which can be visualized more clearly as daily gain relative to average size over the time interval tested, or as

$$RGR = \frac{\dfrac{W_{t2} - W_{t1}}{t_2 - t_1}}{\dfrac{W_{t2} - W_{t1}}{2}}$$

where $1n$ denotes the natural logarithm of weight (W) at time 1 (t_1, for example, birth) or time 2 (t_2, for example, weaning), respectively.

More research is needed to determine the most appropriate selection criteria for optimizing the shape of the growth curve. Apparently, postnatal growth to weaning (adjusted weaning weight-birth weight) or to yearling (adjusted yearling weight-birth weight) ages should be emphasized rather than their respective final weights to eliminate the effect of direct selection for heavier birth weight. Results indicate that although birth weight would still increase because of a positive genetic correlation with postnatal growth, the expected increase in birth weight could be reduced about 30 percent if all emphasis were directed to postnatal growth rate rather than weaning or yearling weight. The increase in mature weight should also be reduced because estimates of the genetic correlation between birth weight and mature weight have been higher than between birth weight and weaning or yearling weight.



Efficiency of gain—differences in amount of feed required to produce a 1,000-pound animal—is an important performance trait in beef cattle.

Efficiency of Gain

Efficiency of gain is one of the traits of greatest economic importance in beef catle. Efficiency of gain is difficult to estimate because it requires individual feeding and adjustments for differences in weight, as increased weight is associated with higher feed requirements per unit of gain.

Present information indicates that genetic improvement can be made in efficiency of gain by selecting for it through rate of gain because the fast gainers will also be efficient gainers. Breeders should depend on differences in rate of gain as an indicator of efficiency of gain rather than incur the added expense of individual feeding. However, if a breeder desires to feed individually and adjust the records for differences in weight to measure differences in efficiency of gain, this is more accurate.

Longevity

The longer animals remain productive in a herd, the fewer replacements will be needed, and thus the costs of growing out replacements to productive age will be reduced. However, the longer an animal remains in a herd, the longer will be the generation interval, which may reduce the rate of genetic improvement from selection. Breeders of purebred cattle or seedstock herds should be concerned with making genetic improvement in longevity

Longevity is important to the commercial producer of beef cattle.

so commercial beef cattle populations will be productive at older ages. Yet, a fairly rapid turnover of generations in purebred herds is desirable for making a maximum rate of genetic improvement in other traits of economic value.

With the trend toward marketing cattle at younger ages, a higher percentage of the beef cattle population must be cows to produce the same amount of beef. This higher proportion of cows makes longevity of greater economic importance from an industrywide standpoint. Longevity can also be important in bulls because it decreases the annual cost of bull service in large herds.

The major factors affecting longevity of cows—or, more important, number of years spent in the breeding herd—are infertility, unsoundness of feet and legs, serious eye diseases such as cancer eye, udder troubles, and unsound mouth. Research shows that susceptibility to cancer eye is heritable, and selection against it should be reasonably effective; however, it is a trait that can be measured only late in life.

Selection for longevity must be confined primarily to such indicators as structural soundness and pedigree information—that is, selection of close relatives of individuals that have had a long productive life. A certain amount of automatic selection for fertility and longevity exists because animals that remain in a herd long enough to produce a large number of offspring have a larger number saved for replacements.

Carcass Merit

Carcass merit is of fundamental importance to the beef cattle industry because desirability of product together with price is the major factor affecting consumption. In selecting for improved carcass merit, the factors that contribute to carcass desirability and their relative importance must be known. Research in many States indicates that the American public desires beef with a high percentage of lean as compared to fat and bone, and the lean must be tender, flavorful, and juicy.

Pounds of edible meat per unit of carcass weight and quality (palatability) of the meat determine carcass value.

Variation in composition of carcasses (relation of lean to fat) is a major factor influencing differences in carcass value. The value of fat trim is negligible in today's market relative to that for retail product (closely trimmed, boneless steaks, roasts, and lean trim) from the carcass. It is not uncommon for carcasses of the same quality grade to range from 10 to 30 percent fat trim. However, differences in composition of this magnitude are due to such environmental sources as age, length of time on feed, and energy content of the ration. Genetic sources of variation are responsible for highly heritable differences in growth of lean, fat and bone, and differences in composition at a constant weight associated with degree of maturity.

Variation in retail product growth (retail product at a constant age) is much greater than variation in composition or proportion of retail product (retail product at a constant carcass weight). Heritability is also higher for retail product growth (60 percent) than for proportion of retail product (40 percent). One study indicated that genetic variation or opportunity to create genetic change was about eight times greater for retail product growth than for proportion of retail product.

Yearling weight (12- to 18-month final weight adjusted for age) is highly related to growth of retail product. The relationship to retail product growth is stronger if an index is used incorporating an accurate measure for less fat thickness along with yearling weight. Results indicate that an index combining yearling weight and less fat thickness is also more highly correlated with postweaning feed efficiency during age or weight constant intervals than yearling weight alone. However, indications are that retail product growth or an index for yearling weight and less fat thickness may be negatively related to degree of maturity at market ages and, consequently, leads to an undesirable shape of growth curve. Thus, the

contribution to total production efficiency from increases in postweaning feed efficiency of growing animals, only part of which are marketed at slaughter, may be offset by subsequently greater maintenance requirements of cows with larger mature size. Therefore, selection for retail product growth or an index for yearling weight and less fat thickness is clearly justified in terminal sire strains or breeds—namely, in strains or breeds from which bulls are used in commercial production on crossbred cows of smaller size to produce progeny for slaughter.

Maximizing muscle development would be desirable in regions of the carcass yielding the more preferred and higher priced cuts—the loin, rib, rump, and round as opposed to the chuck, brisket, plate, shank, and flank. Traditionally, visual appraisal of carcasses or live animals has been used to assess differences in conformation. Morphological differences such as thickness and bulge of the round are quite evident, both within and between breeds. Hypothetically, differences in conformation are associated with variation in distribution of muscle; the amount of muscle could be increased in the round, loin, and rib relative to muscle in other lower priced regions of the carcass. However, within and between breed studies indicated that altering the relative distribution of muscle is not possible in the carcass nor shifting the proportion of muscle to regions of the high-priced cuts. Genetic correlations between proportion of retail product in one cut are high compared with those in all other cuts at a constant carcass weight. Even between breeds, differing widely in conformation (for example, Jersey crosses *versus* Charolais crosses), the percentage of retail product in different cuts relative to total retail product from the entire carcass does not differ significantly.

However, changing the ratio of muscle to fat is possible in the various cuts and the entire carcass. Genetic correlations between retail product and fat trim are strongly negative. Selection for retail product or against fatness can increase the percentage of carcass weight represented by retail product by increasing the muscle to fat ratio in various cuts and the entire carcass.

The Livestock Division, Agricultural Marketing Service (AMS), U.S. Department of Agriculture (USDA), has shown that the yield of closely trimmed, boneless, retail yield from the primal cuts (round, loin, rib, and chuck) can be predicted from the fat thickness at the 12th rib, ribeye area, percentage of kidney and pelvic fat of the carcass, and carcass weight.

AMS prediction equation is as follows: estimated percentage of boneless, trimmed, retail cuts from round, loin, rib, and chuck (cutability) = 52.56 — 4.95 (single thickness of fat over ribeye [12th rib], inches) — 1.06 (percentage of kidney fat) + 0.682 (area of ribeye [12th rib], square inches) — 0.008 (carcass weight, pounds). Also developed is a system that classifies

cattle into five yield grades and identifies differences in estimated yield of boneless, closely trimmed, retail cuts from the primal cuts. These four cuts represent approximately 80 percent of the value of the carcass, and the relation between yield of boneless, trimmed, retailed cuts from the primal cuts and from the rest of the carcass is high. Cattle with a yield grade 1 are superior to those of yield grade 5 in cutability.

In evaluating beef carcasses in progeny or sib tests, use of estimated cutability is recommended because it more accurately accounts for variation in retail product yield than yield grade. Recent results indicate that cutability estimated with the above equation is a relatively poor predictor of differences between breeds that differ widely in size or carcass weight in relation to fat thickness. However, results indicated that the prediction equation ranked animals accurately within each of the different breeds, regardless of their average size. Also, within-breed estimates of the genetic correlation between actual retail product yield and estimated cutability have been high. Thus, estimated cutability is a useful predictor of retail product yield for within breed improvement.

Palatability of beef characterized by differences in tenderness, flavor, and juiciness and other qualitative factors associated with appearance of products over the counter (color, firmness, texture) can have an important influence on consumer acceptance and value of beef. Qualitative traits associated with appearance of products are influenced less by genetic differences than by methods of handling during transportation, slaughter, and conditions during processing and distribution subsequent to slaughter.

In cattle fed, managed, slaughtered, and processed uniformly, tenderness is probably the most important factor affecting palatability of beef. Results indicate that, under these uniform conditions, tenderness has a high heritability. Therefore, if information can be obtained on tenderness, selection for this trait would be an effective way of ensuring that animals will produce tender lean. Tenderness is also related to youthfulness. Therefore, selection of animals that will reach desirable market weights at young ages would be an indirect means to the same end.

In grading carcasses, meat quality is determined by marbling, texture, color, and firmness with maturity. Maturity is evaluated from ossification changes that occur in the skeletal system with advancing age and from color and texture changes in the lean. Among cattle that have been uniformly fed and managed and that are of similar age, marbling is the major determinant of quality grade.

The amount of fat thickness on a carcass is not a factor in determining its quality grade. The observed quantity of outside fat on carcasses is not closely related to their marbling—namely, phenotypic correlations between fat thickness and marbling have been low among carcasses of cattle fed and managed in the

same manner. On the average, however, estimates of the genetic correlation between marbling and retail product yield have been strongly negative, indicating that selection for one trait will reduce the other or that simultaneous selection for increased retail product yield and increased marbling would be ineffective.

The strong negative genetic correlation between retail product yield and marbling found within breeds is consistent with relationships that have been found between breeds representing diverse biological types differing in mature size, growth, and carcass composition at different times, along their weight-age growth curves. Numerous experiments have shown that large growthy breeds have less outside fat and lower degrees of marbling but greater retail product yield than smaller early maturing breeds, when compared at the same age and especially when compared at the same carcass weight.

One experiment involved 1,123 steers by Hereford, Angus, Jersey, South Devon, Limousin, Charolais, and Simmental sires out of Hereford and Angus cows. Although marbling differed significantly between breeds, taste panel evaluations of tenderness, flavor, and juiciness were well above minimum levels of acceptance for all breeds.[3] Differences between breeds in tenderness, when compared at the same age, though significant, were small whereas differences in flavor and juiciness were not significant.

When comparing breed groups at equal ages, tenderness increased slightly as marbling increased. However, when comparisons were made at equal carcass weights, differences in tenderness were smaller and not significant even though differences in marbling were increased. Within breed groups, tenderness declined as cattle were fed longer to increase marbling or fat in the ribeye. As time on feed was lengthened, apparently slight increases in tenderness associated with increased marbling were more than offset by decreased tenderness associated with older age. Thus, the penalty of increased fat trim and cost of production associated with increased time on feed to meet present marbling requirements for the low choice grade are not justified in terms of improvement in eating quality, at least not in cattle fed moderate levels of energy.[4]

Conformation and Its Evaluation

Performance traits other than carcass merit and structural soundness should be measured directly or through the indicators that have been discussed rather than through conformation. Conformation is a performance trait to the extent that it

[3] Steers were fed a ration containing about 71 percent TDN, 60 percent corn silage, 34 percent grain, and 6 percent protein supplement for 7 to 9 months after weaning.

[4] 60 percent corn silage, 34 percent grain, and 6 percent protein supplement.

contributes to carcass merit and longevity. Basically, the important conformation items are structural soundness, which may contribute to longevity, and carcass composition. Research indicates that differences in outside fat can be appraised but with limited accuracy by visual appraisal of the live animal.

When feasible, however, more objective measures of fatness are recommended for assessing differences in composition in live cattle. Ultrasonic measurements of fat thickness or measurements taken with a thermistor probe or a small gage needle are reasonably accurate predictors of carcass fat content.

In bulls developed alike, giving independent scores is reasonable for differences in (1) structural soundness, (2) thickness of natural fleshing or muscling, and (3) outside fat. A muscle score reflects differences in thickness of muscle in relation to length of long bones. Thus, muscle score usually reflects weight in relation to height. With two animals of the same weight and fat thickness but differing in height, the animal with less height will ordinarily receive the higher score for muscling. Preliminary information indicates that mature size may be highly associated with long-bone length at yearling age. Thus, in two animals weighing the same as yearlings but differing in height, the one with the greater height may be expected to have a heavier mature weight and a lower muscling score at yearling age.

On the basis of these preliminary results, selection for heavy weights at yearling age, along with a high muscling score, should result in a growth curve with rapid early growth without excessive mature size. Thus, the use of a muscling score at yearling age may be a factor in affecting mature size. Yearling weight or postnatal growth from birth to 1 year should be given major attention because of its great economic importance. Indications are that near-maximum yearling weight may be obtained along with a high muscling score at yearling age.

CENTRAL TESTING STATIONS

Central testing stations are locations where animals are assembled from many herds to evaluate differences in some performance traits under uniform conditions. Present and potential uses of central testing stations include (1) estimating genetic differences between herds or between sire progenies in gaining ability, grade, finishing ability, and carcass characteristics; (2) determining gaining ability, grade, and finishing ability of potential sires as compared with similar animals from other herds; (3) determining gaining ability, grade, and finishing ability under comparable conditions of bulls being readied for sale to commercial producers; and (4) acquainting breeders with performance testing.

In beef cattle, nutritional level at one stage of life usually has carryover effects on performance at later stages. A poor feed supply in one

period tends to be followed by a period of increased or compensatory gain when rations are improved. Conversely, a higher than normal plane of nutrition, such as that provided by creep-feeding, is likely to be followed by a period of subnormal gains on a normal feeding regime.

Because pretest levels of nutrition and management usually differ from farm to farm or ranch to ranch, performance at a central testing station is influenced by pretest environment. From one standpoint this is a serious disadvantage of central testing stations, as part of the observed differences at a station will be due to pretest conditions. Estimating the importance of these effects is almost impossible, but carryover herd environmental effects are less important than herd differences because of environment when all animals have been fed for a comparable period in the herds in which they were produced. If this is considered, central testing stations minimize herd environmental effects.

Bull buyers must decide from which herds to buy bulls and which bull or bulls to buy within a herd. If the bulls are raised and fed entirely on the farm or ranch where dropped, the buyer has the difficult task of deciding how much of the apparent superiority or inferiority of the bulls is the result of feeding and herdsmanship rather than heredity. When the bulls have spent part of their lives under standard conditions that minimize these effects, the buyer's task is easier, whether he is buying commercial bulls or herd sires for a purebred herd.

Similarly, when progeny test groups of steers from different herds are fed out under standard conditions, to determine the transmitting ability of the sires for growth rate, feed efficiency, and carcass characteristics, sire comparisons are more accurate.

Central tests have limited use for estimating genetic differences among herds—the larger the herd size, the greater the number needed to adequately sample the herd. The precision of these tests is greatly improved when five to eight progeny of each of two or more sires from each herd are tested each year. This permits assessment of within-herd differences to compare with between-herd differences. Furthermore, an adequate sample of animals from each herd should be tested or little valuable information in herd differences will be accumulated.

When central testing stations are used to estimate genetic differences between herds, samples of those completing the evaluation should be used in topcross comparisons in commercial herds so that additional traits can be measured and precision can be increased. When the purpose is to evaluate individual potential sires, bulls should be tested only if they meet rigid qualifications for preweaning rate of gain and conformation score. The number tested per herd or per sire is of no importance; between-herd comparisons should be discour-

aged if numbers from each herd are small.

When the purpose of the testing station is solely to develop bulls and make objective performance information available to prospective buyers, a service especially valuable to small breeders, the number of bulls per herd or per sire is immaterial. To be most useful, however, large numbers should be fed at a single location, giving buyers an adequate number from which to choose. This is possible in commercial-type feedlots.

Influences of pretest environment on test performance probably can never be eliminated, but they can be minimized. Animals should be used whose pretest treatment was similar, and they should be grouped within narrow age ranges. Animals for a given test should be delivered to the station on a specific date and should undergo an adjustment period of 14 to 84 days on the test ration before beginning the official test. The test should run for an adequate length of time—140 to 182 days—if a high-concentrate ration is used the entire time; it should run longer if the ration is high in roughage.

Influences of pretest environment can be minimized in appraisal of results if the final reports include both pretest and test gains. If test gain alone is used, cattle on a suboptimum pretest feeding level that did not permit full expression of their inherent ability to grow are likely to compensate with inflated test gains. Using both pretest and test gains avoids labeling an unduly high test gain as the animal's real gaining ability. This can be done either by averaging pretest and test gains or, if test starts immediately after weaning, by computing a final weight as a standard weaning weight (for example, 205 days) plus test gain. The animal's entire life must be accounted for; "loafing periods" of unequal length, which may influence subsequent gains, should not be omitted.

The problem of compensatory gain is not limited to central testing stations. Within a herd, the inherently fast-gaining calf whose mother was a poor milker is likely to have a low-weaning weight with a correspondingly inflated postweaning gain. Comparisons, whether between herds at test stations or within a herd on an individual farm, should consider both preweaning and postweaning gains.

Central testing stations are most valuable if users recognize that they can evaluate only a limited number of traits and that at best they are only one phase of a complete performance evaluation program. A primary measure of their effectiveness should be the impact they have on increased herd testing for all economically important traits.

HEREDITARY DEFECTS

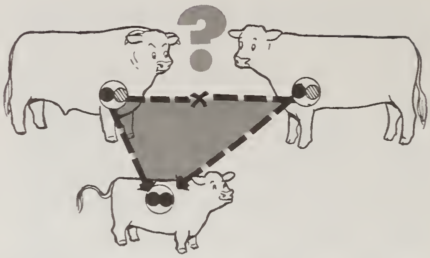
A large number of hereditary defects of possible economic importance have been reported in all breeds of beef cattle and also among the dairy breeds. Perhaps the hereditary defect most widely known is

"snorter" dwarfism, which occurred at troublesome frequencies in some herds in the late 1940's and early 1950's. Discrimination against breeding lines known to carry this defect has reduced its frequency. Snorter dwarfism, like most other hereditary defects, is inherited as a simple recessive—that is, it is caused by a single pair of genes that must be present together before the trait is expressed—and thus it results from the mating of parents that both carry the defective gene.

Other types of hereditary dwarfism are due to different genes. "Comprest" dwarfism seems to result from a gene with incomplete dominance, meaning that the carrier individuals are compressed, and an extreme type of dwarfism segregates from comprest × comprest matings. The comprest condition in Herefords and the compact condition in Shorthorns are probably due to the same gene. Snorter dwarfism has been authentically reported in both the Angus and Hereford breeds; longheaded dwarfism, which is also inherited as a simple recessive, has been reported in the Angus breed.

A practical test of a bull for a specific defective recessive trait is to breed him to females that are known carriers of the gene. Table 5 shows the percentage of bulls that are carriers of a hereditary defect that will not be detected with different numbers of test matings.

To determine whether a bull is a carrier of any genetic defect, bulls may be progeny tested for undesirable recessive genes by either of two methods. Both methods test simultaneously for all recessives.



Hereditary defects should be considered in a constructive breeding program.

One method is to breed by artificial insemination to a large cross section of the female population of the breed. The probability of detecting a carrier of an undesirable recessive is related to the frequency of the gene in the population. The probability of detecting a carrier equals $1-(1-\frac{1}{2}q)^n$ where q is the gene frequency in the female population and n is the number of progeny. This method provides for a short generation interval. Culling animals identified as carriers will be effective in keeping undesirable genes at a low frequency.

The second method involves mating a sire to a group of his own daughters. On the average, to assume that half of the daughters of a bull with a defective, recessive gene will be carriers of that gene (the formula given above applies with $q = .25$) is conservative. The number of sire-daughter matings determines the precision of the test. The percentage of bulls that are carriers of a hereditary defect in-

TABLE 5.—*Testing bulls for hereditary defects inherited as simple recessives*

Matings (number)	Percentage of carrier bulls that will not be detected when mated: To known carriers of a specific defect	To own daughters or to unselected daughters of known carriers of a specific defect
	Percent	*Percent*
5	23.73	51.29
6	17.80	44.88
7	13.35	39.27
8	10.01	34.36
9	7.51	30.06
10	5.63	26.30
11	4.22	23.01
12	3.16	20.13
13	2.37	17.61
14	1.78	15.41
15	1.34	13.48
16	1.00	11.80
17	...	10.32
18	...	9.03
19	...	7.90
20	...	6.91
21	...	6.05
22	...	5.29
23	...	4.63
24	...	4.05
25	...	3.54
26	...	3.10
27	...	2.71
28	...	2.37
29	...	2.07
30	...	1.81
31	...	1.58
32	...	1.38
33	...	1.21
34	...	1.06
35	...	.93

herited as a simple recessive that will not be detected with different numbers of sire-daughter matings is also shown in table 5.

Although many genetic defects are present in beef and dairy cattle and in all classes of farm livestock and probably cannot be eliminated, curbing their effect is possible. Increased frequency of genetic defects in a breed or population can be explained by a gene's producing an effect in carriers that causes them to be preferred to noncarriers; or by chance, a defective gene may happen to be present in a breeding line that is favored and used extensively by the industry. Seedstock producers are in a position to keep these defective genes from becoming a problem to commercial producers by closely observing operations and by realistically approaching a solution once a problem arises. This may require careful screening of herd bulls by progeny testing and promptly eliminating those proved to be carriers of a defective gene.

If an abnormal calf is born, the breeder should establish the most probable cause of the abnormality, which can only be done by complete records. A limited number of developmental abnormalities may occur that do not have a genetic basis. If a breeder decides that an abnormality has a hereditary basis, he should breed away from the source of the trouble. This may be done by outcrossing to a linebred herd, after a careful study of the outcross, so the same or an equally undesirable defect will not be intro-

duced. Another method involves the progeny testing of bulls from his herd to ensure that future herd bulls are not carriers of the gene responsible for the defect. The latter procedure may be indicated if the genetic merit of the herd is high. If only a small percentage of the animals in a herd are possible carriers of the genetic defect, the best course is to eliminate those animals from the herd, provided their genetic merit is not superior to the remainder of the herd.

Although using sons of bulls or cows known to be carriers of defect-producing genes without first progeny-testing the sons is unwise, discrimination against lines of breeding involving animals several generations removed from a known carrier is unjustified. Only one-half of the progeny of a carrier bull will be carriers when the bull is mated to noncarriers. Thus, handling such situations on an individual herd or bull basis is more reasonable rather than discriminating against other herds descended from similar lines of breeding if they are not directly incriminated.

DEVELOPING BREEDING PLANS FOR WITHIN-BREED IMPROVEMENT

Attaining the maximum rate of genetic improvement in all traits of economic value in beef cattle requires a clear perspective of objectives and a planned breeding program for accomplishing them. The different segments of the industry are interested in specific traits, but the breeder must be aware of the demands of the entire industry. The commercial producer wants cows that have long productive lives and wean a high percentage calf crop of heavy, high-grading calves. The feeder demands rapid and efficient feedlot gains, and the packer and retailer are interested in cattle that will produce high-grading carcasses with a minimum of excess fat and the maximum yield of closely trimmed retail cuts from the wholesale cuts of greatest value.

Heritability, genetic association with other traits, and relative economic importance determine the attention each trait should receive in selection. Traits vary in heritability and economic value. The greater the number of traits selected, the smaller the selection differential will be for any one trait. Traits of low heritability respond less to selection than traits of high heritability. The opportunity for selection should be used for traits that will result in the maximum genetic progress for the traits of greatest economic value. Little can be gained and much can be lost by paying too much attention to traits of little economic value and traits of low heritability. Although genetic differences exist between herds, evidence indicates that the large differences in feed resources and management programs between herds make comparing records of different herds difficult. Thus, comparisons should be among animals in the same herd.

Rate of improvement in most economically important traits of beef cattle is slow, primarily because of the inherently low reproductive rate, the large number of traits of economic value, and the long generation interval. The low reproductive rate makes keeping a high percentage of the offspring necessary, especially females, as replacements. The large number of desired traits limits the selection that can be practiced for any one trait. However, most of the economically important traits have reasonably high heritability, fertility being the most notable exception. Though improvement is slow, it is permanent, cumulative from year to year, and transmitted to future generations. Over 15 to 20 years, production in a herd or breed that has been subjected to systematic selection for all economically important traits should be noticeably higher than in herds where no such effort was made.

A systematic performance program with selection based on differences in records is basic to any planned breeding program. The choice of breeding plans involves many considerations. In seedstock herds, a closed-herd program of linebreeding may be desirable when genetic merit is already high, when the herd is large, when the herd is not particularly deficient in some trait of major economic importance, and when the herd is relatively free of hereditary defects. One advantage of a closed herd is that the breeder knows the differences in performance of his own cattle better than another breeder, and he can better evaluate differences in their most probable genetic worth.

In large herds where a relatively large number of sires are used in each generation, a closed herd can be maintained for long periods without any appreciable increase in inbreeding if an attempt is made to avoid the mating of close relatives such as sire-daughter, full brother-sister, and half brother-sister. In herds where as many as 8 to 10 sires are used per generation, the decrease in performance and the reduction in genetic variation as a result of inbreeding will hardly be noticeable.

When the herd is not large and only a small number of sires are used in each generation, the level of inbreeding will increase more rapidly, and performance and genetic variation in the herd will decrease. Decrease in genetic variation decreases the effectiveness of selection.

When the genetic merit of the herd is already high, bringing in an outcross that is genetically superior to some individuals in the herd may be difficult. Also, in herds that are relatively free of genetic defects, the chance of increasing this problem with introductions of outside bulls is greater.

Whenever a genetic defect is troublesome in a herd, or when performance in some economically important trait is particularly low, perhaps an outcross is indicated. Although the outcross should be selected to correct the deficiency, the other traits of

economic value should also receive major consideration. Minimum sacrifice in other traits is a primary objective when bringing in an outcross to correct some deficiency. Outcrossing for any reason in herds of superior genetic merit should be done only on a cautious and systematic basis, and only herds known to be outstanding in the trait of major interest and superior in all traits should be considered. Perhaps this may be another linebred herd. Certainly, records are as fundamental in making selections for outcrossing as they are in making selections from within the herd. After selecting the outcross, a comparison with sires in the herd in a properly conducted progeny test is desirable before extensive use is made of the sires brought into a herd.

In herds that are only average or below in genetic merit, an outcrossing program may logically be the one of choice. However, because most of the opportunity for beef cattle selection is in the bulls used, records in the herds where bulls are selected should be helpful in locating individuals that have superior genetic merit. Securing outcross sires from linebred herds is desirable.

Pedigree, individual performance, and progeny test information all have a place in a constructive breeding program. Young sires should be initially selected on the basis of pedigree and individual performance data. The extent to which they are used in a herd will depend on their rank with other sires based on progeny test information. After progeny test information is available, it should be used in making decisions among sires, remembering that an increase in generation interval is involved. However, in herds of superior genetic merit, where increased accuracy is important, there is justification for using progeny test information more extensively than in herds only average or below average in genetic merit.

Because generation interval affects rate of improvement from selection, it should be kept relatively short. If a bull is superior, he should sire sons that have genetic merit surpassing his own when he is bred to cows comparable in genetic merit to the population that produced him. The problem is one of devising an evaluation program based on use of records that aid in locating such sons. Perhaps one handicap to continued improvement in some herds is the extensive use of an old sire without sufficient attenion to locating sons to replace him. When the old bull passes out of the picture, the herd is left without sires that are superior to him. Continued improvement depends on use of herd bulls that are superior to the ones used in the previous generation.

Before a bull is used extensively in a herd, as would be the case with artificial insemination, progeny testing him for genetic defects on 30 to 35 of his daughters may be desirable. When a herd is following a linebreeding program, the bull to which the linebreeding is directed should not be a carrier of genetic defects,

Herd improvement is accomplished by replacing a sire with his superior sons.

and known carriers should be discarded.

Breeding cattle of superior genetic merit is a great challenge. Many decisions must be made on breeding plans and in selecting herd bulls and replacement females. One difficult decision seems to be dropping a bull that still has a good market for his progeny, even though the breeder may have determined that the bull is not contributing to the breeding goals and may be inferior to others in the herd.

The more a breeder knows about the animals in his herd and the more clearly he understands his objectives, the more frequently he should make correct decisions. Success in breeding superior beef cattle, like success in other ventures, depends primarily on the utility of the goals and the accuracy of decisions while working toward the goals. A complete performance program provides the basis for making correct decisions. Goals can be attained only by a planned breeding program based on the systematic use of records for selection on all traits of economic value. Successful breeders have not been faddists but have exercised common sense and good judgment with the long-term outlook in mind.

CROSSBREEDING FOR COMMERCIAL BEEF PRODUCTION

Crossbreeding can be used in commercial beef production (1) to provide for heterosis and (2) to combine and match breed characteristics with market requirements, feed, and other resources available in specific herds. First, the genetic basis for heterosis will be discussed, followed by a review of results from crossbreeding experiments. Then drawing on results of experiments to date, important considerations in planning crossbreeding programs and alternative crossbreeding systems will be discussed.

Genetic Basis for Heterosis

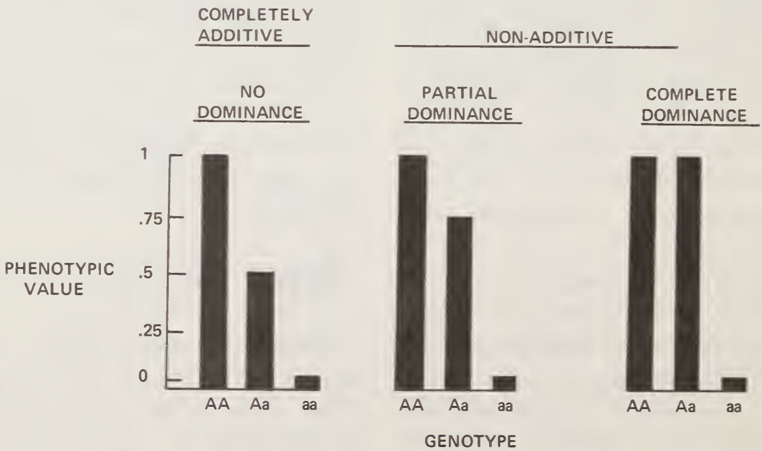
Nonadditive gene effects, which are caused by interaction of genes, occur when specific gene pairs or combinations produce favorable effects from being present together.

Examples of nonadditive gene effects are shown below for interactions between genes of a single pair or different degrees of dominance.

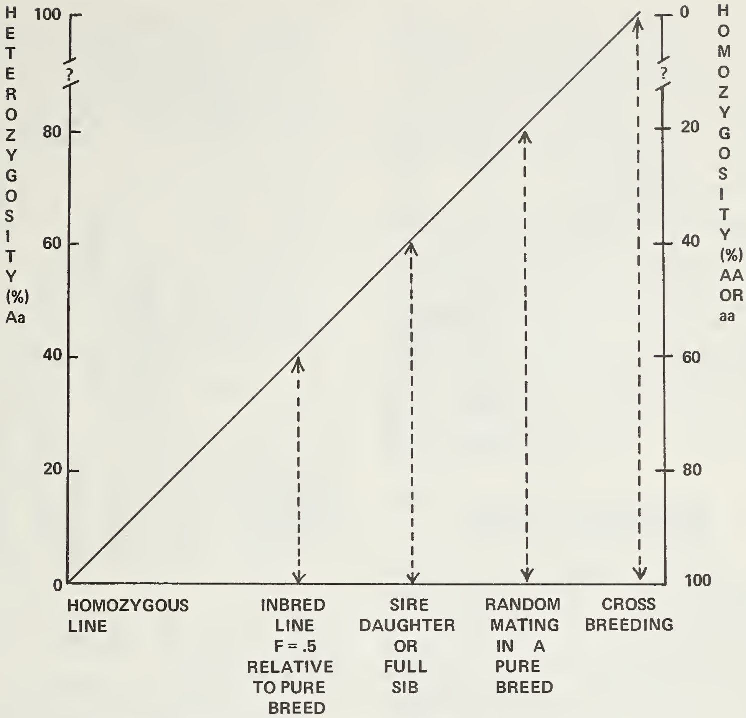
The first graph portrays a completely additive case of no dominance. The heterozygous genotype (Aa) is intermediate in phenotypic value to the homozygous genotype (AA or aa). Coat color in Shorthorns is an example of completely additive inheritance. Red animals are homozygous (both genes of each pair are alike) for the red gene (RR), white animals are homozygous for the white gene (rr), and roan animals are heterozygous (Rr, genes of the pair are unlike).

The second graph portrays a nonadditive case of partial dominance, and the third graph portrays a nonadditive case of complete dominance. Many examples of complete or nearly complete dominance exist in cattle where the heterozygote (Aa) has the same or nearly the same appearance as the homozygote for the dominant gene (AA) but is different from the homozygote for the recessive gene (aa). For example, polledness is dominant to horns, black coat is dominant to red, and normal size is dominant to dwarfism. These are examples of qualitative traits whose inheritance is controlled by single gene pairs. Such quantitative traits as growth rate and carcass merit are controlled by many pairs of genes, parts of which may be additive or nonadditive.

The importance of nonadditive gene effects on quantitative traits has been studied through crossbreeding and inbreeding. This study is possible because pure breeds are more homozygous (AA or aa) than breed crosses, and inbred lines within pure breeds are more homozygous than purebreds. The figure (page 51) shows homozygosity and heterozygosity expected in pure breeds and inbred lines with crossbreds.



Effects of different degrees of dominance in phenotypic value.



Effects of inbreeding on heterozygosity or homozygosity.

Inbreeding means mating animals more closely related to each other than the average relationship in the population. Primarily, inbreeding makes pairs of genes homozygous and lowers the percentage of heterozygous gene pairs. This is why sire-daughter matings are often considered to test for deleterious recessives such as dwarfism. Inbreeding in offspring from sire-daughter matings is 25 percent relative to the pure breed involved. Thus, the proportion of heterozygous "carriers" (Aa) resulting from sire-daughter matings is reduced 25 percent, and half of these may emerge as homozygous recessives (aa), exposing any deleterious recessive traits carried by the sire.

One study showed that rather intensive inbreeding occurred during the formation of Shorthorns and that inbreeding continued to accumulate slowly until, by 1920, the inbreeding coefficient for an average animal was 26 percent. This means that the average Shorthorn in 1920 had 26 percent fewer heterozygous gene pairs than the average of those animals used to form the breed.

A study of Hereford pedigrees indicated that the average inbreeding coefficient increased by 8.1 percent in 12.9 generations from 1860 to 1930. Thus, with inbreeding increas-

ing 0.68 percent per generation from 1860 to 1930, inbreeding would be expected to be about 15 percent today relative to those in 1860. Similar rates of inbreeding have been found for other breeds.

Generally, studies about the levels of inbreeding are not available because records of early matings are fragmentary. Because of geographic barriers, considerable inbreeding probably occurred long before herd books and pedigree barriers were established. Early breeders may have used the Bakewell system, which encouraged mating of close relatives to increase prepotency, fix type, and form uniform and distinct breeds of cattle. Even after breed populations became established, inbreeding, or homozygosity, slowly increased with time. Although the exact extent to which breeds are inbred is not known, conservative estimates show that purebreds are at least 20 percent more inbred or less heterozygous than their crosses. This level of inbreeding is assumed in the figure, page 51, and table 6 to demonstrate nonadditive effects of genes on performance of crossbreds, purebreds, and inbred lines.

Differences in inbreeding or proportion of heterozygosity have no effect on average performance of crossbreds, purebreds, or inbreds when gene effects are completely additive (table 6). However, with any degree of dominance, partial or complete, the mean performance of crossbreds is greater than that of purebreds. Similarly, performance of inbred lines would be expected to decline relative to pure breed or line crosses within a pure breed. This phenomenon is called *inbreeding depression*. It is caused by nonadditive effects of genes and reduction in heterozygosity in inbred lines that uncover undesirable recessives, which otherwise would be concealed or partially concealed by dominant genes. Its reverse, heterosis, is the difference in performance between crosses and the average of the parental breeds or lines used in the cross. Heterosis is caused by nonadditive effects of genes when heterozygosity

TABLE 6.—*Average expected performance of crossbred, purebred, and inbred lines with additive and nonadditive gene effects*[1]

Mating type	Zygotic frequency relative to crossbreds (percent)[2]			Additive gene effect	Non-additive gene effects	
	AA	Aa	aa		Partial dominance	Complete dominance
Crossbred	0	100	0	.5	.75	1.0
Purebred	10	80	10	.5	.70	.9
Sire-daughter	20	60	20	.5	.65	.8
Inbred line (F = .5)	30	40	30	.5	.60	.7
..Do	40	20	40	.5	.55	.6
Homozygous line	50	0	50	.5	.50	.5

[1] Phenotypic values shown on page 50 are assumed to compute the averages.

[2] Average expected frequency over a large number of gene pairs.

is restored to the pure breed level by crossing inbred lines within a breed or when heterozygosity is established at an even higher level by crossing breeds.

Explanation of heterosis could be expanded to include more complex nonadditive genetic models. However, this explanation provides sufficient understanding of heterosis to formulate crossbreeding systems to be discussed in subsequent sections. Fortunately, one need not depend entirely on theory. A number of experiments have been conducted concerning the importance of nonadditive gene effects on inbreeding depression and heterosis in cattle.

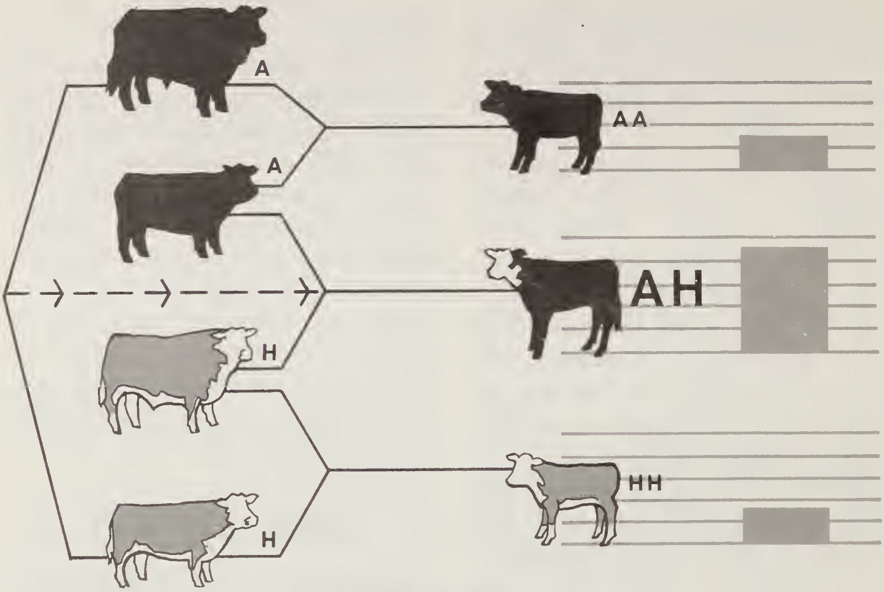
Considerable experimental evidence indicates that nonadditive genetic variation is important. A recent comprehensive study was made on 48 inbred lines from 8 State agricultural experiment stations and a USDA Research Location in the Western Region, Project (W-1). Results indicated that, on the average, fertility (percentage of cows pregnant) declined 2 percent and 1.3 percent with each 10-percent increase in inbreeding of the dam and calf, respectively. Percentage calf crop weaned declined 1.6 percent and 1.1 percent with 10-percent increments in inbreeding of the dam and calf, respectively. Results also have indicated that inbreeding has depressing effects on growth of calves and maternal ability. These results indicate that nonadditive gene effects are important and cause a decline in performance when homozygosity is increased at the expense of heterozygosity by inbreeding.

On the opposite side of the coin, crossbreeding experiments have indicated that heterosis is of significant economic importance in beef cattle. Although the results vary some for specific traits from different experiments and from crosses of different breeds, they generally show significant effects of heterosis on postnatal survival, preweaning and postweaning growth, puberty age, and fertility and mothering ability of crossbred cows.

Effects of Heterosis

Results of heterosis in beef cattle have been consistent with results in swine, sheep, and poultry and indicate that the level of heterosis (nonadditive genetic variation) is inversely proportional to heritability (additive genetic variation). Thus, in such high heritability traits as postweaning growth rate, feed efficiency, and carcass composition, the level of heterosis is low; whereas in traits with low heritability, such as livability and fertility, effects of heterosis are large.

Following is a summary of a crossbreeding experiment conducted in three phases by USDA and Nebraska researchers involving Herefords, Angus, and Shorthorns. Phase I concerning individual heterosis expressed by the crossbred calf and phase II concerning maternal heterosis expressed by the crossbred cow were conducted at the Fort Robinson Beef Cattle Research Station, Craw-



HETEROSIS

Effect of heterosis on some performance traits is important. The size of the bars at the right show that, because of heterosis, productivity in some traits is greater in crossbred, or crossline animals than in the average of the parental breeds or strains.

ford, Nebr. Phase III, at the U.S. Meat Animal Research Center, evaluated the level of heterosis restored from one generation to the next by alternative systems of crossbreeding.

In phase I, the three straightbreds and all reciprocal crosses among Herefords, Angus, and Shorthorns were produced for four calf crops. Heterosis, or hybrid vigor, was evaluated by comparing the crossbreds with the average of the straightbreds. Crossbred and straightbred calves were sired by the same purebred bulls and out of comparable straightbred cows. The study included 393 crossbred and 358 straightbred calves sired by 16 Hereford, 17 Angus, and 16 Shorthorn bulls. A series of economically important traits were studied, including those presented in table 7. The effects of heterosis were significant for most of the traits evaluated.

No difference was shown between crossbred and straightbred calves for percent calf crop born, but early postnatal survival was significantly greater in crossbreds. Crossbred calves were 4.6 percent heavier at weaning (7 months) than straightbreds. The combined advantages in survival and growth rate accounted for an 8.5 percent advantage in weight of calf weaned per cow in favor of crossbred calves over straightbred calves.

Essentially no difference in feed

TABLE 7.—*Effects of individual heterosis in Herefords, Angus and Shorthorns from phase I of Fort Robinson experiment*[1]

Item	Crossbred calves	Straightbred calves	Heterosis Difference	Heterosis Percent
Number of matings	470	447		
Calves born ....percent..	89	89	0	—
Calves alive at 2 weeks ....do....	86	82	4	—
Calves weaned ....do....	84	81	+ 3	—
Birth wt ....pound...	74.2	71.5	2.7	3.8
Weaning wt at 200 days ....do....	437.4	418.0	19.4	4.6
200-day wt/cow exposed ....do....	367.4	338.6	28.8	8.5
Steers:				
Postweaning daily gain ...do....	1.845	1.794	0.052	3.0
452-daily wt ....do....	912	883	29	3.3
TDN/gain	5.76	5.77	— .01	— .1
Retail product ....pound[2]..	331	320	11	3.4
Retail product ....percent..	63.4	63.9	— .5	— .9
Carcass grade[3]	10.2	9.9	0.3	—
Retail product/unit TDN	0.1345	0.1338	+ .0007	0.5
Net merit ....dollar[4]..	220.33	211.52	8.81	4.2
Heifers:				
2-year-old management[5]				
Postweaning daily gain ..pound..	1.173	1.100	0.073	6.6
550-day wt ....do....	853	805	48	6.0
Age at puberty ....days...	321	356	—35	9.8
Wt at puberty ....pound..	580	587	— 7	1.2
3-year-old management[6]				
Postweaning daily gain ..pound..	0.985	0.910	0.075	8.2
550-day wt ....do....	764	712	52	7.3
Age at puberty ....days...	382	422	—40	9.5
Wt at puberty ....pound..	528	534	— 6	1.1

[1] From Gregory *et al.*, J. Anim. Sci. 24:21; 25:290; 25:299; 25:311 and Wiltbank and others, Journal of Animal Science 25:744; 26:1005.

[2] Pounds closely trimmed, boneless cuts from the carcass.

[3] Grade of 9 = high good, 10 = low choice, USDA grades.

[4] Net merit is value of retail product (dollars) minus feed costs from weaning to slaughter.

[5] Heifers managed and developed to calve as 2-year-olds were born in 1962 and 1963 and fed about 4 pounds of concentrate feed per head per day during their first winter.

[6] Heifers managed and developed to calve first as 3-year-olds were born in 1960 and 1961 and fed 1 pound of 40% protein supplement per head per day during their first winter.

efficiency existed between crossbred and straightbred steers. The crossbred steers produced slightly fatter carcasses that graded higher when slaughtered at the same age. However, when adjusted for differences in carcass weight, no differences showed in carcass composition. Thus,

if they had been slaughtered at the same weight, the carcasses would have been the same in composition.

In net merit (value of the boneless, closely trimmed retail meat, adjusted for quality grade, minus feed costs from weaning to slaughter), the advantage of the crossbred steers over the straightbred steers was $8.81 (1965) per carcass. This net merit difference is among the steers that lived to slaughter. The 3 percent advantage for the crossbreds in calf crop weaned was not involved in computing this difference.

The effects of heterosis on postweaning growth rate of heifers on lower levels of feeding were greater than in steers on a growing fattening ration. Effects of heterosis decreased with age after approximately 1 year. Age at puberty (first heat) for crossbreds was 35 and 40 days younger than straightbred heifers. A moderate level of feeding was associated with 2-year-old first calving and a low level of feeding with 3-year-old first calving, respectively.

Straightbred and reciprocal cross females produced at Fort Robinson in phase I of the experiment involving Angus, Herefords, and Shorthorns were retained to evaluate maternal heterosis for reproduction and maternal traits in phase II. Straightbred and reciprocal cross females of each pair of breeds were compared when they were mated to the same sires of a third breed. For example, to evaluate maternal heterosis in Angus-Shorthorn reciprocal crosses, the performance of Angus-Shorthorn and Shorthorn-Angus cows was compared with that of Angus and Shorthorn straightbred cows when the cows in all four groups were mated to the same Hereford bulls.

Over 6 breeding seasons, 570 matings of straightbred cows and 687 matings of crossbred cows produced spring calf crops from 1963 through 1968. Approximately half of the cows were managed to calve first as 2-year-olds and half as 3-year-olds to evaluate the effects of maternal heterosis in cows aged 2 through 6 years and 3 through 8 years in each management regime.

Calf crop weaned was 6.5 percent greater for crossbreds than straightbreds (table 8) because of higher pregnancy and first-service conception rates in the crossbreds. When crossbred and straightbred cows were both raising crossbred calves, differences in postnatal survival were small in the second phase of the experiment.

Effects of maternal heterosis were 1.7 percent for weight at birth, 3.6 percent for weight at 135 days, and 4.7 percent at 200 days (weaning). Effects of maternal heterosis reflect greater and more persistent milk production favoring crossbreds over straightbreds by 0.9 percent at 2 weeks postpartum, 7.5 percent at 6 weeks, 6.1 percent at about 14 weeks, and 38 percent at weaning at about 29 weeks postpartum. Actual weaning weight was 14.8 percent greater per cow exposed to breeding for crossbreds than for straightbreds, on the average, over both management regimes for combined effects of ma-

TABLE 8.—*Effects of maternal heterosis in Herefords, Angus and Shorthorns from phase II of Fort Robinson experiment*[1]

Item	Crossbred cows	Straightbred cows	Heterosis Difference	Heterosis Percent
Number of matings	687	570		—
Conceived 1st service ....percent[2]..	63.2	56.6	6.6	—
Pregnant end breeding ....do[2]....	91.5	85.9	5.6	—
Pregnant in fall ....do[2]....	89.7	84.5	5.2	—
Full term calf ....do[2]....	87.2	81.1	6.1	—
Live calf born ....do[2]....	86.2	80.4	5.8	—
Live calf 2 weeks ....do[2]....	84.4	77.8	6.6	—
Live calf weaned ....do[2]....	81.6	75.2	6.4	—
Calving to 1st estrus ....days...	53.6	56.3	— 2.7	—
Conception date, Julian date	156.3	159.1	— 2.8	—
Gestation length ....days...	284.7	283.5	1.2	—
Calving date, Julian date	76.0	77.6	— 1.6	—
Calf weight:				
Number calves	555	420		
Birth wt ....pounds..	76.4	75.2	1.2	1.6
135 days ....do....	338.0	326.3	11.7	3.6
Weaning, 200 days ....do....	453.1	434.6	18.5	4.3
12-hour milk production ....do....				
2 weeks	6.79	6.73	.06	.09
6 weeks	7.55	7.02	.53	7.5
June (approx. 14 weeks)	7.91	7.45	.46	6.2
Weaning (approx. 29 weeks)	3.31	2.40	.91	37.9
200-day wn wt/cow ....pounds[2]..	379.3	333.0	46.3	13.9
Actual wn wt/cow ....do[2]....	392.5	341.8	50.8	14.8

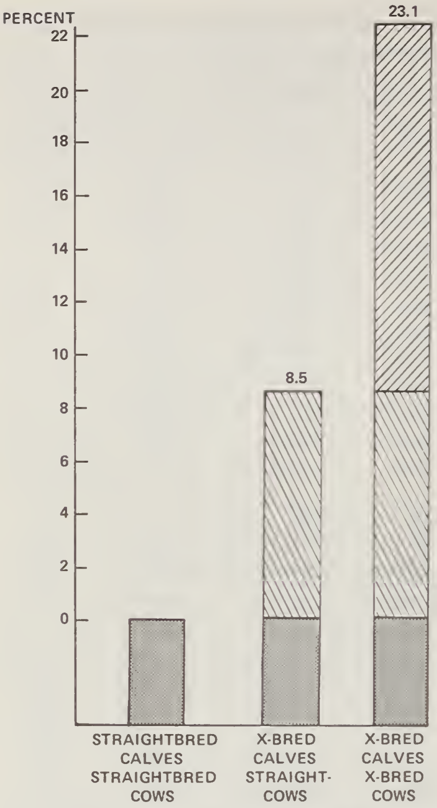
[1] From Cundiff, Gregory and Koch, 1974a,b. Journal of Animal Science 38:711; 38:728.
[2] Based on all cows exposed to breeding: 687 cow-year-matings for crossbred females and 570 cow-year-matings for straightbred females.

ternal heterosis on reproduction and maternal ability.

Preliminary results indicate that further advantages will accrue through greater longevity and lifetime production of crossbreds than with straightbreds. The experiment was terminated when cows involved in phase II ranged from 12 to 15 years. Twenty-four percent of the original crossbred heifers assigned to breeding pastures to initiate phase II remained in the breeding herd until the end of the experiment (1975) compared to 11 percent of the straightbreds.

For growth, feed efficiency, and carcass traits, the heterosis effect was greater in the Hereford-Angus and Hereford-Shorthorn combinations than for the Angus-Shorthorn. For age, weight at puberty and maternal performance, the effect of maternal heterosis was greatest for Hereford-Shorthorn reciprocal crosses.

When the advantages of individual heterosis on survival and growth



Cumulative heterosis effects for pounds of calf weaned per cow exposed.

of F_1 calves (phase I) and the advantage of maternal heterosis on reproduction and maternal ability of crossbred cows (phase II) are all combined, weight of calf weaned per cow exposed to breeding was increased 23 percent. More than one-half of the increased performance from heterosis was attributable to use of crossbred cows.

These results are typical of other experiments. Results from a Virginia experiment involving the same British breeds varied for specific traits, but the total effect of heterosis on pounds of calf weaned per cow is similar. Results from USDA, Montana, Missouri, and Ohio experiments involving Charolais, Angus, and Herefords, and from Iowa involving Herefords, Angus, Brown Swiss, and Holsteins have shown effects of heterosis similar to those summarized in tables 7 and 8 for most traits. Differences in effects of heterosis between specific crosses have not been significant in these experiments. Even higher levels of heterosis have been reported from experiments involving Brahman-British breed crosses in Texas, Louisiana, and Florida.

Combining Breed Characteristics

Additive genetic differences between breeds are responsible for performance differences between breeds managed in the same environment. Experiments have shown that substantial differences exist between breeds for such traits as milk production, growth, mature size, and carcass composition at points along growth curves. These differences are caused by differences between breeds in the frequency of genes affecting each trait that have emerged as a result of diverse selection goals (for example, beef *versus* dairy), natural selection for adaptation in different environments, and genetic drift (chance).

Crossbreeding can be used to optimize gene frequency and combine desired characteristics in cross-

breds that would not be possible in any parent breed alone. This can be done effectively because heritability of differences between breeds is high. Heritability represents the differences observed between animals transmitted to their progeny. Because breeds differ in average performance for a given trait, differences between animals of different breeds are more heritable than differences of the same magnitude within a breed because progeny regress to different breed means. This is partly caused by inbreeding that has occurred in the evolution of breeds to increase the genetic likeness or uniformity within breeds and the distinctness of differences between breeds.

Experiments involving crosses between Brahmans and Angus, Herefords or Shorthorns in the Southern Region (Louisiana, Florida, Texas, Georgia and South Carolina) were the first to use additive as well as nonadditive genetic effects to combine desired characteristics of different breeds. Brahman-British breed crosses combine the heat and insect tolerance of the Brahmans, which evolved in the tropics, with the desired carcass characteristics including carcass grade and tenderness of the British breeds. These traits, combined with the substantial effects of heterosis on survival and growth of calves and fertility and maternal ability of cows, have resulted in more productive crossbreds for beef production in the Southern Region than the parent breeds.

Experiments involving Charolais top crosses at Louisiana and heterosis experiments involving Charolais, Angus, or Herefords conducted by the USDA and Montana and agricultural experiment stations at Ohio and Missouri, focused further attention on crossbreeding to combine characteristics of breeds. Effects of heterosis in these experiments have been similar to those in British breed crosses for growth and carcass traits. However, results have demonstrated that Charolais cattle are superior to Herefords and Angus in preweaning and postweaning growth rate, produce carcasses with higher percentages of lean, and contain less fat at comparable ages. Although straightbred Charolais have graded one- to two-thirds of a quality grade lower than Herefords or Angus, respectively, the grades of Charolais-Hereford and Charolais-Angus crosses have been only slightly lower than those of Hereford-Angus crosses. These experiments indicate that Charolais-British breed crosses do combine characteristics of both breeds in a desired direction; more specifically, the cross increases growth and percentage of retail product and reduces fat trim of the British breeds and improves carcass quality grade of the Charolais. Results such as these stimulated importation of new continental European breeds into North America via quarantine facilities in Canada beginning in the late 1960's.

An extensive Germ Plasm Evaluation Program began at the U.S. Meat Animal Research Center in 1969. It includes a number of these and other domestic breeds formerly con-

sidered only for dual purpose or dairy production. This program extends the evaluation of crossbreeding to a broad range of biological types represented by breed characteristics such as milk production, growth, mature size, and carcass composition at points along their growth curves. The major objective is to characterize breeds representing different biological types in different feed environments and production situations for the full spectrum of biological traits relating to economic beef production. The program is conducted in cycles involving crossbreds by different sire breeds out of Hereford and Angus cows compared to control populations of Hereford-Angus reciprocal crosses.

The first cycle involved breeding Hereford, Angus, Jersey, South Devon, Limousin, Simmental, and Charolais bulls (20 to 35 sires per breed) by artificial insemination (AI) to Hereford and Angus cows (from 2 to 7 years old at calving) to produce three calf crops in March, April, and early May of 1970, 1971, and 1972.

All male calves were castrated shortly after birth, weaned in October or November at approximately 205 days, fed out on a ration containing about 71 percent TDN, and slaughtered after an average of 212, 247, and 279 days on feed. Detailed carcass data have been obtained in cooperation with Kansas State University. Results from the most recent report on the three calf crops produced in the first cycle of this program are summarized in table 9 according to sire breed. All of the calves by Jersey, South Devon, Limousin, Simmental, and Charolais sires were F_1 calves out of Hereford and Angus dams; thus, comparisons to Herefords and Angus should be made with Hereford-Angus reciprocal crosses to account for the average effect of heterosis.

A high degree of calving difficulty cannot be tolerated in commercial beef production. Not only is the expense of labor for assistance at calving a prohibitive factor, but results from this experiment indicated that conception rate in the subsequent breeding season was reduced 16 percent by calving difficulty (85.3 percent for cows not experiencing difficulty *versus* 69.4 percent for cows experiencing difficulty). Also calf mortality at or near the time of birth was four times greater in calves experiencing difficult parturitions than in those not experiencing difficulty (11.5 percent *versus* 3.1 percent).

Breeds siring the heaviest calves (Charolais, Simmental, Limousin, and South Devon) experienced more calving difficulty than those sired by Hereford, Angus, and Jersey sires, graphically illustrated (page 62). The incidence of calving difficulty was associated with birth weight. On the average, calving difficulty increased .74 percent for each pound increase in birth weight. The association between calving difficulty and birth weight relative to sire breed was strong in 2-year-old first calf Angus and Hereford heifers and was also present to a lesser degree in 3-year-

TABLE 9.—*U.S. Meat Animal Research Center germ plasm evaluation program breed group means for calves produced in cycle 1*[1]

Item	HH&AA	AH&HA	JH&JA	SDH&SDA	LH&LA	SH&SA	CH&CA
	Breed group[2]						
Steers and heifers prewn.:							
Number of births	307	375	302	232	371	399	382
Birth wt ....pounds...	72.3	74.3	64.6	78.9	79.8	83.8	85.1
Calving difficulty ....percent..	15	11	5	27	24	29	34
Adj. 200-day:							
wt ....pounds...	410	428	404	428	432	450	456
ratio[3]	95.8	100.0	94.4	100.0	100.9	105.1	106.5
Steers postwn.:[4]							
Number	150	204	132	94	173	176	176
Daily gain ....pounds...	2.44	2.47	2.29	2.65	2.38	2.73	2.76
Final wt, 457 days ...pounds...	970	1001	951	1024	1014	1072	1087
TDN/unit gain:[5]							
0 to 217 days	5.83	5.99	6.24	5.90	5.78	5.91	5.70
530 to 1,035 lb	6.37	6.12	6.79	5.96	5.87	5.69	5.39
0 days to 5 percent fat	5.77	5.71	6.03	5.82	6.44	6.11	5.98
Dressing ....percent..	63.3	63.6	62.3	64.1	64.3	62.8	63.6
Retail product ......percent[6]..	66.5	65.5	64.9	67.0	71.8	70.2	71.2
Fat trim ....percent..	21.3	22.5	22.7	20.6	15.8	16.4	15.8
Bone ....percent..	12.2	12.0	12.4	12.3	12.5	13.4	13.0
USDA Qual. grade[7]	11.8	11.9	11.9	11.9	10.8	11.2	11.4
T.P. accept[8]	7.3	7.3	7.4	7.4	7.2	7.3	7.4
T.P. tenderness	7.3	7.4	7.5	7.5	7.0	6.9	7.4
Heifers postwn.:							
Number	126	132	117	120	161	157	132
200-day ADG ....pounds...	0.97	1.07	0.90	1.17	1.10	1.15	1.15
400-day wt ....do....	591	629	561	651	640	671	671
550-day wt ....do....	673	715	656	741	713	757	768
Pub. age ....days...	390	371	322	364	398	372	398
Pub. wt ....pounds...	582	585	482	603	642	629	667
Pregnant ....percent..	80.2	93.0	86.4	85.1	82.0	86.2	80.6

[1] From Progress Report No. 3, U.S. Meat Research Center, Agr. Res. Serv., USDA, ARS-NC-41, April 1976.

[2] First letter denotes sire breed and second letter denotes dam breed where H = Hereford, A = Angus, J = Jersey, SD = South Devon, L = Limousin, S = Simmental and C = Charolais.

[3] Ratio computed relative to Angus-Hereford and Hereford-Angus controls.

[4] Except for TDN/unit gain, means are adjusted to a starting age of 240 days and 217 days on feed. The finishing ration contained 60% corn silage (71.2% TDN, 12% crude protein).

[5] Intervals for evaluation of TDN/unit gain begin after a 25 to 30 day conditioning period (0 days) or at 530 lb live weight and end after 217 days on feed, 1035 lb. live weight, or 5 percent ribeye fat corresponding to USDA choice quality grade.

[6] Retail product, % = actual yield of boneless, closely trimmed beef from carcass.

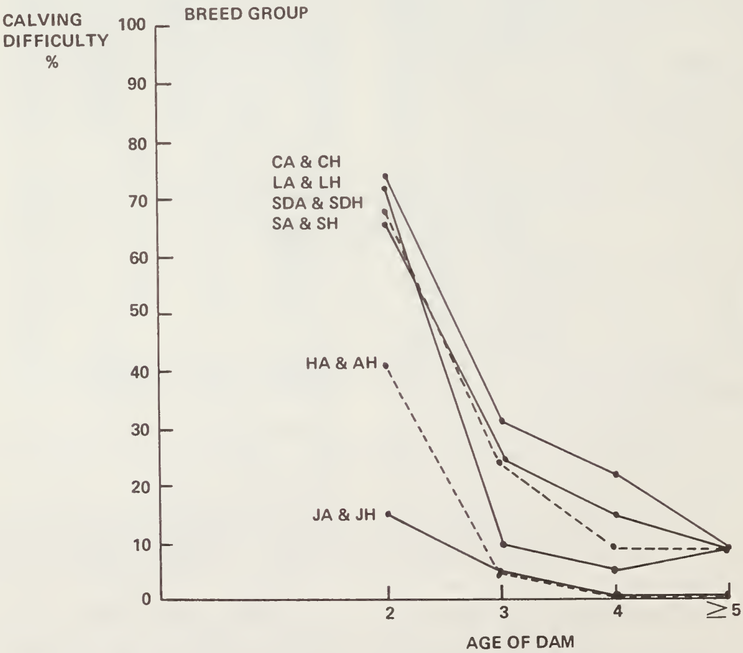
[7] USDA Quality grade: 10 = average good, 11 = high good, 12 = low choice, etc.

[8] Taste panel scores based on a 9-point hedonic scale, with higher scores indicating greater acceptability (72 per sire breed).

old cows. The incidence of calving difficulty was much lower in 4- and 5-year-old Angus and Hereford cows. These effects were substantial and should be considered when developing a crossbreeding program.

Substantial differences are indicated among sire breeds for preweaning and postweaning growth rate (table 9). Weaning weight ratios relative to Hereford-Angus reciprocal crosses range from 94.4 percent for Jersey to 105.1 percent and 106.5 percent for Simmental and Charolais crosses, respectively. Similar results were found in average final weight.

Feed efficiency (TDN per unit gain, table 9) was evaluated over age constant (0 to 217 days on feed), weight-constant (530 to 1035 lb), and grade-constant (0 days to 5 percent fat in the ribeye muscle) intervals. The range between breed groups was greatest for the weight constant interval. Breed groups with the most rapid growth rates required less feed per unit of gain than slower gaining earlier fattening breed groups because fewer days of maintenance were required in weight constant intervals. The ranking and relative differences of breed groups for feed efficiency in the age constant interval (0 to 217 days postweaning) were similar to that for



Calving difficulty in Hereford and Angus cows according to sire breed of calf and age of cow. (Smith et al. 1976. U.S. Meat Animal Research Center, Agr. Res. Serv., USDA. Journal of Animal Science 43:27.)

the weight constant interval, but the range and differences between breed groups were smaller. On an age constant basis, the larger, faster gaining breed groups that were heaviest at weaning maintained more weight throughout the 217 days. In spite of heavier weights maintained, larger breed groups producing the leanest carcasses were the most efficient in the age constant interval.

Feed efficiency from weaning (except for 25- to 30-days adjustment) to a grade constant end point (0 days to 5 percent fat in the ribeye muscle) is also shown in table 9. The amount of fat in the ribeye muscle selected as an end point was 5 percent because this level of fat approximated the marbling required for cattle of these ages to achieve a quality grade of USDA choice. To a grade constant end point, Hereford-Angus crosses were significantly more efficient than Limousin and Simmental crosses.

The other breed groups did not differ significantly from Hereford-Angus crosses. On a quality grade constant basis, breed groups reaching 5 percent fat content in the ribeye muscle in the shortest number of days were the most efficient. However, feed efficiency to a quality grade constant basis does not take into account differences in value or amount of beef produced relative to feed consumed by the Hereford and Angus cows producing all breed groups. Also, evaluation to a grade constant end point assumes that feeding to higher levels of fatness is justified in terms of improving eating quality. Taste panel evaluation of flavor, juiciness, tenderness, and overall acceptability taken on these cattle indicated that this assumption was not justified.

Charolais, Simmental, and Limousin crosses had a higher percentage of retail product and less fat trim than other breed groups when evaluated at the same age (table 9). Differences in composition were even greater when evaluated at the same carcass weight. When evaluated at the same grade, the differences among breed groups were smaller, but Charolais, Simmental, and Limousin crosses had a higher percentage of retail product than other breed groups. Jersey crosses were the lowest.

No significant differences were found among breed groups for flavor or juiciness evaluated by taste panel. Tenderness and overall acceptability were also evaluated on a scale from 1 to 9, with higher scores indicating greater tenderness or acceptability. All breed groups were well above minimum levels of acceptance for tenderness and overall acceptability when evaluated at the same age (table 9), carcass weight, or quality grade end points. When comparing breed groups at equal ages, tenderness increased slightly as marbling increased. However, when comparisons were made at equal carcass weights, differences in tenderness were smaller even though differences in marbling were increased.

Within breed groups, taste panel tenderness declined as cattle were fed for longer periods to increase

marbling or fat in the ribeye. As time on feed was lengthened, apparently slight increases in tenderness associated with increased marbling were more than offset by decreased tenderness associated with older age. Thus, the penalty of increased fat trim and cost of production associated with increased time to meet marbling requirements for the low choice quality grade appeared not to be justified for improved eating quality—at least not in cattle fed moderate levels of energy (71 percent TDN) for 7 to 9 months after weaning.

Differences among breed groups in postweaning growth of heifers up to 18 months (table 9) were similar to those found in steers. As in previous experiments, a sizable effect of heterosis for age at puberty was observed in Hereford-Angus reciprocal crosses relative to straightbred Herefords and Angus. South Devon, Simmental, and Hereford-Angus crosses all reached puberty at similar ages, which were significantly older than Jersey crosses but significantly younger than Charolais or Limousin crosses.

Results indicate that sire breeds of large size and rapid growth rate or breeds that produce lean carcasses can be mated to cows of medium size to increase weight and value of retail product from carcasses per unit of feed consumed by the progeny from weaning to slaughter. When matings are considered as terminal crosses (that is, if all progeny from the large sire breeds are slaughtered), total production efficiency will be increased because cows of medium size are used to produce progeny, and feed requirements are not increased for maintenance of the cow herd. The advantages of terminal crosses are tempered by a high degree of calving difficulty, particularly in cows calving at 2 and 3 years. Calving difficulty takes a heavy toll in calf crop percentage through reduced survival of calves and reduced rebreeding performance of cows. However, in cows calving at mature ages, calving difficulty has not been a serious problem.

Assessing the relative merits of various biological types for the full spectrum of economic traits including fertility, maternal ability, and productive efficiency would be premature although evaluation on reproduction and maternal perfor-

TABLE 10.—*Angus-Holstein crossbred heifers compared to Angus heifers under range conditions in Oklahoma*[1]

Item	Angus	Angus × Holstein
Number of cows	27	23
200-day total milk production ..pounds ..	1,753	2,505
Weight before calving ......pounds ..	760	870
Weight after weaning .....pounds ..	753	814
Weight change ....pounds ..	−7	56
Rebreeding, during 90-day breeding season ....percent..	63	13

[1] From Deutscher and Whiteman. 1971. Journal of Animal Science 33:337.

mance is in progress. Intensive experiments are being initiated to evaluate nutrient requirements to support growth, maintenance, lactation, and reproduction among different biological types varying in size and milk production. A major objective is to develop an understanding relating to optimizing such biological factors as cow size, milk level, and so forth, and to maximize reproduction and productive efficiency in different feed environments and production situations.

Synchronizing Genetic Resources With Feed and Other Production Resources

Significant differences in characteristics such as growth, carcass composition, mature size, and milk production exist between breeds. At the same time, vast differences are noted between quantity and quality of feed supply from one region of the United States to another. Stocking rates range from one cow per 2 acres to only a few cows per section of land. Even within a region large differences are noted between quantity and quality of feed supply from one operation to another. These differences are often determined by such resources as water, fertility, variety of grasses, forages, crops or crop residues available or supplied to provide the nutrient base for the beef operation.

Just as engines that vary in horse power and performance require different quantities and quality of fuel to maximize efficiency, so do cattle that vary in performance capability require different quantities and quality of feed to provide their requirements for growth, maintenance, lactation, and reproduction to maximize feed conversion and other resources into beef. This has been demonstrated in recent experiments involving breeds varying in size and lactation potential.

In an experiment conducted under range conditions in Oklahoma (table 10), Angus-Holstein heifers were compared to Angus heifers when both groups were wintered on a relatively low level of supplement. Winter supplemental feed consisted of 2 lb/head/day of cottonseed meal from November 15 to April 15 and 5 lb/head/day of prairie hay from January 1 to April 15. Angus-Holstein heifers produced significantly more milk but lost significantly more weight in the subsequent breeding season during lactation than Angus. Of 23 Angus-Holstein F_1 heifers and 27 Angus heifers that calved in the spring as 2-year-olds, only 13 percent of the Angus-Holstein heifers rebred whereas 63 percent of the Angus rebred during a 90-day natural service breeding season.

A more recent experiment at Oklahoma involving Hereford, Hereford-Holstein crosses, and straightbred Holsteins fed different levels of supplement primarily during lactation has provided further evidence that reproduction is reduced when additional nutrients to support greater requirements for growth, maintenance, and lactation of larger cows

with higher lactation potential are not met (table 11). Two levels of winter supplementation were fed to each breed group through the winter beginning in the fall at calving. An additional group of straightbred Holsteins was fed a high level of supplement. Average size and particularly milk production differed markedly between these breed groups. As supplement levels increased, weight loss during lactation decreased and cows tended to exhibit estrus and conceive earlier. This trend has been more pronounced in the breed groups of larger size and higher lactation potential.

Holsteins represent an extreme biological type characterized by high milk production and large size. Milk production has increased from selection practiced for a long time, especially during the last 30 years, when selection has been intensified by extensive progeny testing and artificial insemination. This has been accompanied by changes in dairy herd management that include high levels of supplemental grain fed in relation to level of milk production. Similar relations among nutrient intake, reproduction, size, and lactation exist, presumably to a lower degree, among breeds that differ by a narrower range in milk production and size, or both. Experiments are in progress involving different biological types to partition differential requirements for growth and maintenance from those for lactation while providing for maximum reproduction.

Regarding size, recent results from studies involving individual feeding of progeny and cows conducted at Ohio, South Dakota, Texas, and Wisconsin indicate that cow size does not significantly influence total efficiency of beef produced. For example, in the Ohio study involving cows of different size within and among Hereford, Hereford-Angus, Hereford-Charolais, and Charolais breed groups, results indicate that progeny of larger cows both within and between breeds produced more edible beef. However, these differences were offset by greater feed consumption of the larger cows and their progeny. Thus, conclusions show that cow size was of minor importance in determining total efficiency of edible beef production.

Although understanding in this area is not complete, current results point to a need for synchronizing genetic resources with feed and other production resources. Similar considerations are important in such growing-finishing segments of production as optimal efficiency of growth and carcass composition to meet consumer and market requirements. When planning a crossbreeding program, choose breeds that are adapted to the feed and other resources available to maximize economy of production in the herd or specific operation.

Important Considerations in Planning Crossbreeding Programs

Substantial effects of heterosis can be used through crossbreeding:

TABLE 11.—*Performance of Hereford, Hereford × Holstein and Holstein females as influenced by level of winter supplementation under range conditions with fall calving*[1]

Item	Hereford		Hereford × Holstein		Holstein		
	Moderate	High	Moderate	High	Moderate	High	Very high
			2-year-olds				
Total winter suppl. ....pounds[2]..	434	731	515	882	595	945	1203
Precalving wt ....pounds..	885	904	988	995	1151	1090	1116
Mid-lactation wt ....do....	753	788	813	882	946	917	954
Post lactation wt ....do....	985	983	993	1055	1152	1156	1200
Daily milk yield ....do....	12.0	12.9	17.3	19.3	23.5	24.5	28.4
Postpartum interval ....days[3]...	71	62	82	68	83	71	65
Fraction conceiving[4]	12/12	12/12	13/13	13/13	8/11	9/11	11/11
Calf wean. wt ....pounds[5]..	507	500	550	563	604	621	634
			3-year-olds				
Total winter, supp.	353	691	343	763	390	780	1189
Precalving wt ....pounds..	1012	1022	995	1073	1187	1172	1210
Mid-lactation wt ....do....	850	832	812	897	912	955	1011
Post lactation wt ....do....	1035	1046	1011	1092	1168	1172	1240
Daily milk yield ....do....	13.4	13.2	17.7	22.4	31.2	27.8	31.0
Postpartum interval ....days...	72.7	68.3	79.3	66.2	126.7	78.5	57.7
Fraction conceiving	12/12	9/10	8/11	12/13	4/4	8/9	8/8
Calf wean. wt ....pounds..	601	592	645	641	723	736	730
			4-year-olds				
Total winter, supp.	221	565	263	564	313	626	891
Precalving wt ....pounds..	990	1030	1096	1051	1272	1183	1212
Mid-lactation wt ....do....	796	891	857	865	968	968	1056
Post lactation wt ....do....	1011	1066	1034	1055	1218	1146	1244
Daily milk yield	13.4	13.5	20.4	20.2	25.5	29.8	26.2
Postpartum interval	58	51	69	58	83	91	63
Fraction conceiving	16/19	17/18	15/17	17/19	6/15	9/16	15/16
Calf wean. wt ....pounds..	574	576	625	659	732	699	692

[1] From Animal Science and Industry Research Reports 1972, MP-72; 1973, MP-90; and 1974, MP-92; Agricultural Experiment Station, Oklahoma State University and USDA, Agr. Res. Serv.

[2] Soybean meal (44%), 60.1%; milo, ground, 30.3%; dehydrated alfalfa meal, 5.0%; dicalcium phosphate, 2.9%; Masonex, 1.3%; salt, 0.5%; plus vitamin A added at 10,000 IU/lb of supplement.

[3] Number of days from calving to first observed estrus.

[4] Fraction conceiving is number of cows conceiving/number of cows raising a calf during the breeding season.

[5] Adjusted for sex of calf and to an average weaning age of 240 days.

(1) Results with Hereford, Angus, and Shorthorns indicate that heterosis can increase pounds of calf weaned per cow in the breeding herd 23 percent.

(2) Crossbreeding programs should involve crossbred cows because more than half of this advantage is dependent on their use.

Crossbreeding can also be used to combine desired characteristics of breeds and synchronize genetic resources with feed and other resources:

(1) In certain situations, large size breeds with lean carcasses can be mated to cows of small to medium size to increase efficiency of production; that is, to increase amount and value of retail product relative to calf and cow feed costs.

(2) Advantages of mating sires of large size to cows of medium size are tempered by a high degree of calving difficulty when the cows are calving at 2- and 3-years of age.

(3) To avoid calving difficulty and associated calf crop losses from calf mortality and reduced rebreeding, cows should be mated to bulls of other breeds that are similar in size until they are 4 years of age or older. In cows calving at 4 years or older, calving difficulty has not been a serious problem.

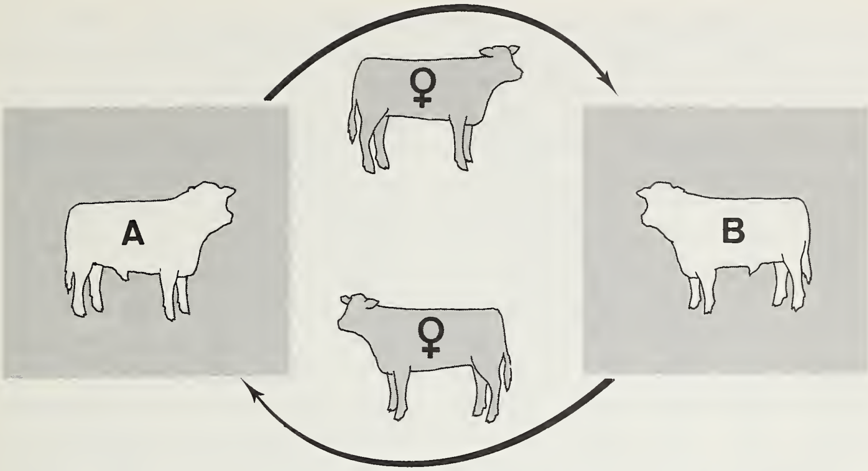
(4) Maternal breeds of which the cow herd is comprised should be well adapted to the climatic-feed environment and production situation.

(5) Nutrient demands to support growth, maintenance, and lactation of the cow herd need to be stabilized from one year to the next in most situations.

CROSSBREEDING SYSTEMS

Poultry and plant breeders of many species such as corn may use static mating systems that produce sufficient hybrids for complete use of heterosis in commercial production. Using hybrid vigor can be maximized in these species because only a small proportion of the total population is involved in seedstock production. Heterosis use is more difficult in cattle because of their low reproductive rate and long generation interval, which overlaps from one year to the next. However, this does not preclude utilization of a high level of heterosis in commercial beef production. Crossbreeding systems can be used that restore significant levels of heterosis from one generation to the next. These systems can also use additive genetic variation between breeds to synchronize genetic resources with feed and other production resources.

The crossbreeding system of choice is not universal. It is dependent on such resources specific to each operation as number of cows in the herd, number of breeding pastures, facilities, labor availability and amount and quality of feed supply. Practically any crossbreeding system is feasible with artificial insemination when adequate facilities, labor, and technical expertise are available to accommodate a successful artificial insemination program. Because artificial insemination is not always



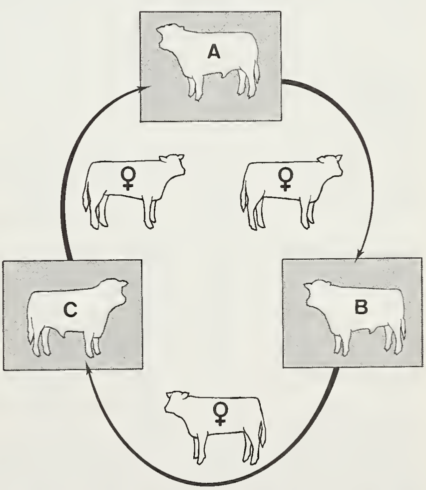
A two-breed rotation. Heifers sired by breed A are mated to bulls of breed B, and heifers sired by breed B are mated to bulls of breed A. Pounds of calf per cow increased about 15 percent.

feasible, discussion of crossbreeding systems will include use of bulls in natural service. The following discussion is intended to be reasonably complete regarding the basic systems of crossbreeding; however, modifications are often necessary to optimize use of heterosis in any specific operation.

Rotational Systems

Rotational systems of crossbreeding have been used in commercial swine production for years. The systems commonly implemented in commercial beef production are diagramed in figures on this page.

In the two-breed rotation, the program is initiated by mating cows of breed A to bulls of breed B. Heifers from these matings are mated to bulls of breed A. The next generation heifers by breed A are mated to bulls of breed B, and so forth, generation after generation. Thus, a minimum of two breeding pastures are required for this system, and heifers must be identified by breed of their sire.



A three-breed rotation. Pounds of calf per cow increased about 20 percent.

In the three-breed rotation, the same pattern is involved except a third breed is included. Heifers sired by breed A are mated to bulls of breed B. Replacement heifers from these matings are bred to bulls of breed C, and the resulting heifer progeny kept for replacement are mated to bulls of breed A, and so forth. In a three-breed rotation at least three breeding pastures are required, and heifers must be identified according to the breed of their sire.

Rotational systems restore a substantial level of heterosis from one generation to the next. Tables 12 and 13 show the genetic composition and level of heterosis expected in each generation as two- and three-breed rotations continue. The level of heterozygosity in calves and cows fluctuates in rotational systems during the initial generations. However, once crossbred cows have entered the system, fluctuation is hardly noticeable in performance level because heterozygosity of the calf and heterozygosity of the dam are both important, low levels in one are offset by high levels in the other. Thus the average level of heterosis expected from a two-breed rotation is 67 percent of the maximum of when an F_1 cow is mated to sires of a third breed, and levels of performance from heterosis do not fluctuate much once crossbred cows have entered the system.

The level of heterosis sustained by a three-breed rotation is higher than that in a two-breed rotation because the relation between bulls and cows mated is remote. The three-breed rotation sustains an average level of 86 percent of the maxi-

TABLE 12.—*Genetic composition and level of heterosis expected in a two-breed rotation*

Generation	Sire	Additive genetic composition: Dam A	Dam B	Calf A	Calf B	Heterozygosity: Dam	Calf	Calf weight weaned per cow exposed[1]
		Percent	*Percent*	*Percent*	*Percent*			*Pounds*
1	A		100	50	50	0	100	8.5
2	B	50	50	25	75	100	50	19.0
3	A	25	75	63	37	50	75	13.8
4	B	63	37	69	31	75	62	16.4
5	A	69	31	66	34	62	69	15.1
6	B	66	34	67	33	69	66	15.8
7	A	67	33	67	33	66	67	15.9
8	B	67	33	67	33	67	67	15.5
Average		50	50	50	50	67	67	15.5

[1] Based on heterosis effects of 8.5% in a crossbred calf and 14.8% in a crossed cow observed in phase I (table 7) and phase II (table 8) of the Fort Robinson Heterosis Experiment assuming that heterosis is directly proportional to heterozygosity. Experiments are in progress to determine the veracity of this assignment.

TABLE 13.—*Genetic composition and level of heterosis expected in a three-breed rotation*

Generation	Sire	Additive genetic composition						Heterozygosity, percentage		Calf weaning weight per cow exposed[1]
		Dam			Calf					
		A	B	C	A	B	C	Dam	Calf	
1	A			100	50	0	50	0	100	8.5
2	B	50	0	50	25	50	25	100	100	23.3
3	C	25	50	25	12	25	62	100	75	21.2
4	A	12	25	62	56	12	31	75	88	18.5
5	B	56	12	31	28	56	16	88	88	20.4
6	C	28	56	16	14	28	58	88	84	20.1
7	A	14	28	58	57	14	29	84	86	19.8
8	B	57	14	29	29	57	14	86	86	20.0
Average		33	33	33	33	33	33	86	86	20.0

[1] Based on heterosis effects shown in tables 7 and 8.

mum heterozygosity realized in the second generation when the F_1 cow is mated to sires of a different breed. Once crossbred cows enter the system, performance caused by heterosis increases substantially; in subsequent generations, performance level from heterosis fluctuates little.

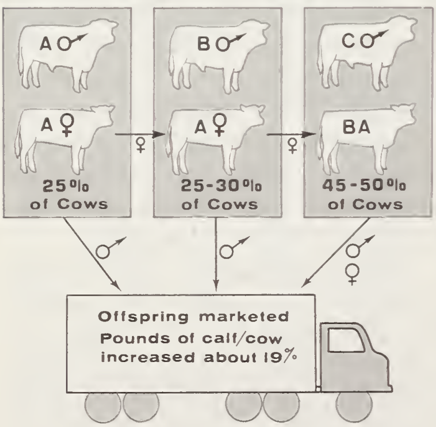
Additive genetic composition, on the other hand, fluctuates greatly in two- or three-breed rotations being highest for the most recent sire breed and lowest for the most remote. For example, in the eighth generation of a three-breed rotation (and on the average overall generations), 57 percent of a cow's genes are of the breed of their sire, 29 percent are of their grand sire, and 14 percent are of their great-grand sire, the latter being the same as the breed to which they are to be mated. Because of this, rotational systems must involve breeds with comparable characteristics such as birth weight, size, and lactation potential, and are well adapted to the feed and other production resources of the operation. Comparability is necessary to avoid calving difficulty and associated calf crop losses, which can be a serious problem in cows that calve at 2 and 3 years of age and that have been mated to bulls of a breed that are substantially larger. Also, using breeds that are comparable in size and milk production is important to stabilize nutrition and management requirements in the cow herd. Using comparable breeds is especially important when feeding and managing each group separately is not feasible according to size and lactation potential (as well as age when supplemental feeding is required).

Rotational systems have an advantage over some other systems because all replacement heifers are provided from within the system. Opportunity to select replacement heifers intensely can be greater in rotational systems than in straight-

breeding systems because of the higher percentage calf crop weaned and the greater longevity of crossbred cows. However, genetic improvement within the herd is still determined by the sires selected within each breed. Bulls selected for use in rotational crossbreeding should be selected just as judiciously as those selected in straightbreeding or any other crossbreeding system.

Static-Terminal Sire Systems

In this system straightbred cows of one breed (A) are mated to a second sire breed (B) to produce F_1 crossbred females (BA). The F_1 crossbred females are mated to a third breed (C) and the progeny, both male and female, are marketed; hence the name terminal sire. The object of this system is to maximize production efficiency by selecting breeds used in the sequence of matings that complement each other to the highest degree.



Static three-breed cross system.

The first two breeds (A and B) in the sequence should be selected to synchronize cow size and maternal performance with available feed resources. They need not be comparable in both respects as long as the sequence shows that calving difficulty is not a problem. For example, one breed can be of larger size with lower milk production potential and the other of smaller size with higher milk production potential provided the feed requirements of the resulting F_1 females are about the same as those of breed A or can otherwise be provided for economically in the operation.

Rate and efficiency of gain and carcass composition should be emphasized in breed C, the terminal cross, to maximize these characteristics in as many progeny marketed as possible. The primary advantage of this system is that pounds of beef marketed can be increased per unit of feed consumed by both the cows and the calves.

However, the above advantages may be offset by considerable sacrifice of heterosis in this system. A high percentage of the cows (approximately 25 percent) must be mated as straightbreds to meet replacement requirements for straightbreds in the system. In addition, at least 25 percent of the cows in the herd must be straightbreds (A) mated to produce F_1 heifers for herd replacements that are mated to the terminal sire breed. Thus, the advantages of greater fertility and increased maternal performance of crossbred cows are sacrificed in at

least 50 percent of the herd, and the advantages of individual heterosis on survival and growth of F_1 calves are sacrificed in the straightbreds produced that comprise 25 percent of the herd. Maximum heterosis is realized only in the terminal cross, which comprises about 50 percent of the cows in the system.

Another disadvantage of the static-terminal sire system is that little selection pressure can be applied among female replacements entering the cow herd. Nearly all females (about 90 percent) produced by the straightbred cows are required as replacements when the number of cows in the herd is to be maintained. This percentage can be altered by increasing the proportion of straightbred cows to crossbred cows, but it deducts from the benefits of heterosis and complementary characteristics. The cost of sacrificing selection pressure in females is often overemphasized, however, because the impact of selection on the herd is determined primarily by the bulls selected to produce the heifers. Research has shown that 80 to 90 percent of the genetic improvement in a herd is attributable to sire selection. Selection pressure among sires can and should be just as great in a static terminal sire crossbreeding system as in any other mating systems. The characteristics receiving primary emphasis in selection should differ from one breed to the other and correspond to the characteristics that each breed contributes to the system.

A static-terminal sire system does require at least three breeding pastures as indicated (page 72). However, to avoid calving difficulty in 2- and 3-year-old F_1 crossbred females, a smaller sire breed requiring a fourth breeding pasture or backcross matings to one of the maternal sire breeds (A or B) for the first and second calvings may be necessary. Using the fourth sire breed permits maximum heterosis, but the backcross matings would only sacrifice some of the individual heterosis in the calves produced and is probably easier to manage in most situations.

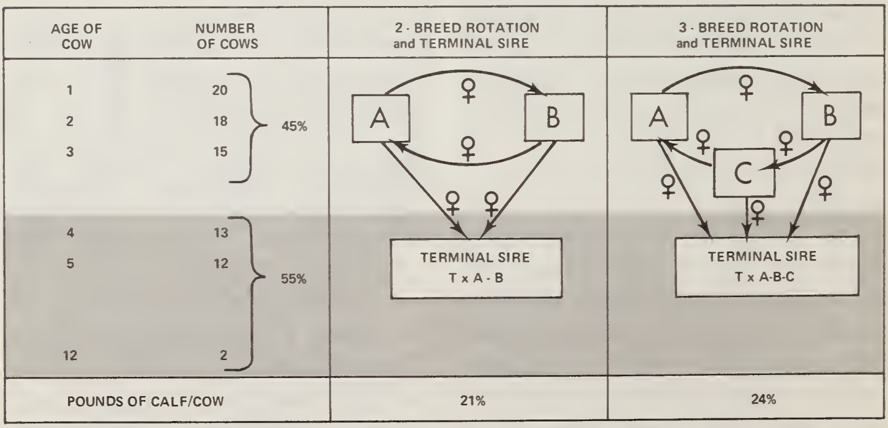
Assuming levels of heterosis shown in tables 2 and 3 and the terminal sire breed increases in calf weaning weight of 5 percent, pounds of calf marketed per cow in the breeding herd should be increased about 18 to 19 percent over straightbreeding by this system. This is similar to the production level shown for a three-breed rotation (table 8). The sacrifice in heterosis is partly offset by the additional growth expected from use of a terminal sire and because a high percentage (42 percent) of the calves marketed are by terminal sires. If technology were available to control sex of offspring, this system would have much more to offer; however, with present technology, the static-terminal sire system appears to have no more to offer than a three-breed rotation. Thus, the system of choice will depend on personal preference, marketing considerations, and ease of management in specific operations.

Rotational-Terminal Sire Systems

Some operations combine most of the advantages of rotational systems with those of a terminal sire system. Rotational-terminal sire systems involve rotational mating of maternal breeds in a portion of the herd to provide female replacements for the entire herd. A portion of the replacements are mated to a terminal sire breed as outlined in the illustration below. In most herds, at least 45 percent of the cows will have to be mated in the rotational portion of the program to meet requirements for heifer replacements. The other cows in the herd (50 to 55 percent) would be mated to a terminal sire breed selected to excel in rate and efficiency of growth and carcass composition. The object of the system is to maximize efficiency of production in terms of pounds of calf or beef produced per unit of feed consumed by calves and cows in the herd.

To achieve maximum benefit from the system, the breeds used in the rotational portion of the program should be small to medium and selected to synchronize maternal performance with feed and other production resources available in the operation. Because a rotational crossing system is employed, the maternal breeds should be reasonably comparable in size and milk production to minimize calving difficulty and to stabilize nutrition and management requirements in the cow herd.

The rotational crossing portion of the program should involve the youngest cows in the herd. In many instances 1-, 2-, and 3-year-old females comprise 45 percent of the breeding females in a herd. However, 4-year-old cows can be involved in the rotational crossing when they are needed to maintain or increase herd size. In this way cows are not mated to a terminal sire breed of large size until they are 4



Rotational-terminal sire crossbreeding system (100 cows calving and 20 yearling heifers are assumed).

years or older when the incidence of calving difficulty is low and not a serious problem.

Again, as in the static-terminal sire program, nearly all of the heifers produced in the rotational portion of the program are required as replacements. This may be offset, however, by heifers from young cows. Research at several experiment stations has shown that maternal performance of females raised by young cows is greater than that of females raised by mature cows. This may be caused by heifer calves fattening as a result of the favorable maternal environment associated with greater milk production of mature cows compared with younger cows. Fat deposition may interact with mammary and udder development in the growing female to reduce subsequent milk production of females raised by mature cows relative to those raised by young cows. This interrelationship can be used to advantage if the youngest cows in the herd are employed in the rotational system to provide female replacements for the herd.

The terminal sire breed would be selected to excel in growth rate and efficiency and to transmit superior carcass composition to his offspring. Female offspring from the terminal sire breed would not be kept for replacement, which would avoid increased feed requirements for maintenance that would result when large cows were kept in the herd. Both the male and female offspring from the terminal sire would be marketed.

Either the two-breed or the three-breed, rotational-terminal sire system requires a high level of management. Cows must be identified by breed of sire and birth year. The two-breed, rotational-terminal sire system requires three breeding pastures. The three-breed, rotational-terminal sire system can be run with four breeding pastures or, if bulls of the maternal sire breeds (A, B, and C) are replaced by bulls of the next breed in the sequence after only 2 years use, then this system can be run with only two breeding pastures. This is because all females will be 4, 5, or 6 years old before bulls of the same breed as their sire are scheduled for use in the rotation. At these ages, the cows are scheduled to be mated to the terminal sire breed. This is not possible in the two-breed, rotational-terminal sire system because the females are still young (2, 3, or 4 years) and in the rotational portion of the herd when bulls of the same breed as their sire are scheduled for use in the rotation. Thus, in herds as small as 50 or 60 cows, the three-breed, rotational-terminal sire system is feasible provided two breeding pastures are available. In this system about 70 percent of the calves marketed are males and females from the terminal sire matings and about 30 percent are steers from the rotational matings.

Assuming that the terminal sire breed increases growth rate 5 percent and that the levels of heterosis in two- and three-breed rotations are as outlined in tables 7 and 8, pounds of beef produced per cow in the

breeding herd should be increased to levels of 21 percent and 24 percent over straightbreeding in the two-breed and three-breed, rotational-terminal systems, respectively. This percentage is more than the static-terminal sire system or the rotational systems described earlier. The three-breed, rotational-terminal system provides greater production than the two-breed, rotational system because greater heterosis is sustained by the system.

Small Herd Systems

In herds of small size with only one breeding pasture, none of the systems described above are feasible. However, these systems can be used to maintain a substantial level of heterosis. For example, a high level of heterosis can be restored from one generation to the next by using three sire breeds in rotation and replacing sire breeds every 3 years. Heterosis will approach the maximum level if replacements are kept from the last two of each three calf crops produced by each sire breed used in the rotation. A still higher level of heterosis will be realized if a fourth breed is included in the rotation. The feasibility of this is usually determined by the availability of desirable herd bulls from four breeds that are comparable in size and lactation potential and compatible with available feed and other production resources.

Systems that are most commonly recommended for small, single-sire herds involve purchase of crossbred females for replacement requirements. Quite often this system is the simplest and easiest to manage when a good source of crossbred females can be identified. Larger breeders using good management and sire selection in two- or three-breed rotations of breeds, which are adapted to the feed resource base in the small herd, are an excellent source for replacement females for small single-sire operations. Production level from heterosis will be the same as outlined earlier for two- and three-breed rotations, and growth of the calves will be determined by the sire performance level in the small herd. As the cows become mature, a sire breed capable of transmitting rapid and efficient growth can be used to increase production to the level characterized by the terminal-sire systems discussed above.

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